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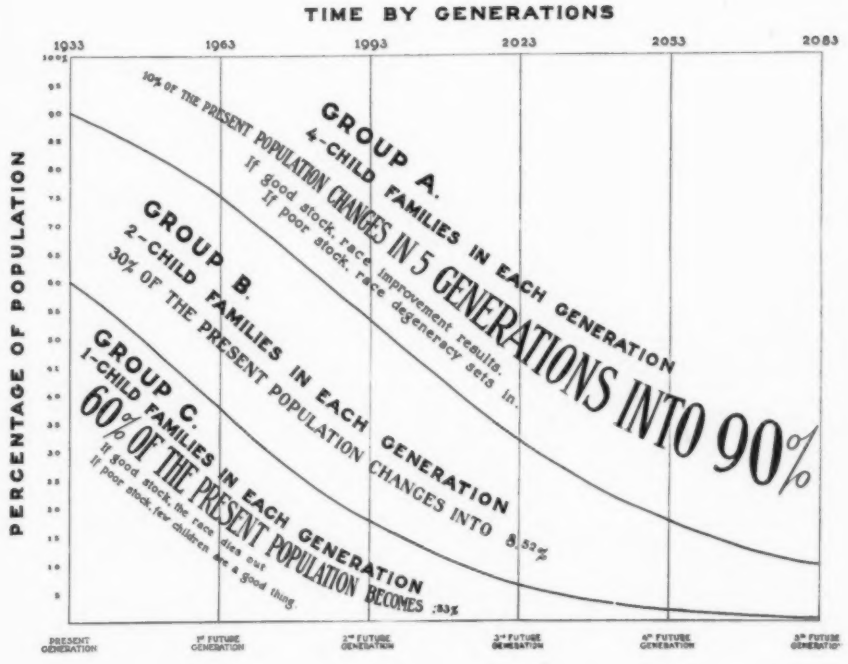

HOW FAMILY-SIZE AFFECTS RACIAL FORTUNES

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Methods of Locating Genes in Salivary Chromosomes

A Maize Hybrid Combining Three Genera

Inheritance of Extra Fingers and Toes

The Future of the White Race

VOLUME 26 APRIL, 1935 NUMBER 4

The American Genetic Association

An incorporated organization devoted to promoting a knowledge of the laws of heredity and their application to the improvement of plants, animals, and human racial stocks

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Maps and Slides of Salivary Chromosomes

MAPS of the giant salivary chromosomes form the groundwork for much new research and are of great value as instructional material as well. The two maps published in the Journal (in the December, 1934, and February, 1935, issues) are offered, unfolded, on heavy paper for mounting or framing, at the following prices:

Painter's cytogenetic map of the salivary chromosomes, 9½ by 18 inches, line-cut showing major chromosome details and the genes approximately located to end of 1934—Postpaid ..... 50 cents

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DID THE ANCESTOR OF MAIZE HAVE "EARS" LIKE THIS?

Frontispiece

The origin of maize has proved more of an enigma than that of any other crop. Maize is the only species of the genus Zea, and the two nearest relatives would have to be classified as distant cousins. (See Figure 1.) Perhaps the immature "ears" shown here bear some resemblance to those of the progenitor of maize. These ears are produced by a triple hybrid combining in one plant complete sets of the chromosomes of the three existing American genera of the botanical tribe Tripsaceae. It is possible that this plant may show ancestral reversion to the extent that different genes of the three component genera are complimentary to each other.

A TRIGENERIC HYBRID OF ZEA TRIPSACUM AND EUCHLAENA

All of the Chromosomes of Maize and Its Two Nearest Relatives Combined in a Single Plant

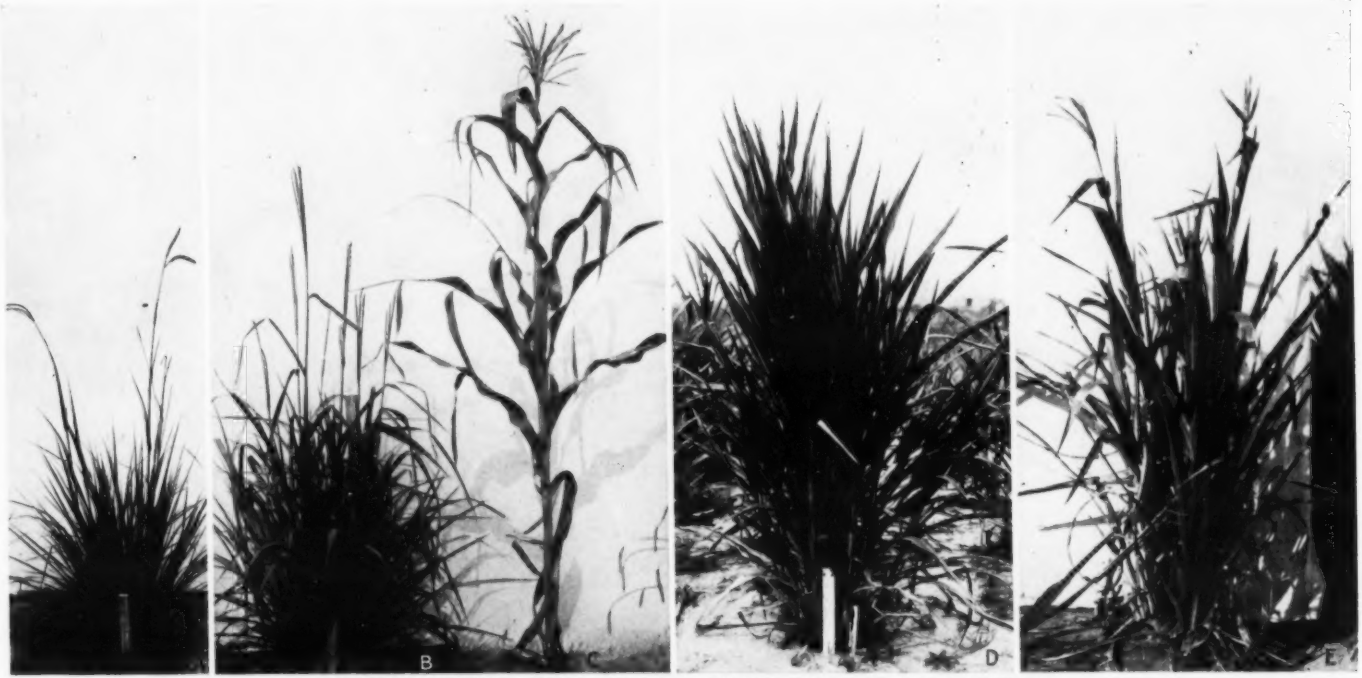
P. C. MANGELSDORF and R. G. REEVES
Texas Agricultural Experiment Station

IN a previous paper in this JOURNAL[9] we reported the hybridization of maize with *Tripsacum dactyloides*, one of the native grasses of North America, which has long been recognized as a relative of maize. We also attempted, as reported briefly in this paper, to cross Tripsacum with Euchlaena, the only other American relative of maize, but were not able to obtain viable seeds. Small abortive seeds of this cross were produced which, upon cytological examination, proved to be true hybrids, but in no case were we successful in securing living hybrid plants of Tripsacum and Euchlaena though we have since made numerous additional attempts. We have, however, now succeeded, by a less direct method, in combining the germplasm of Tripsacum and Euchlaena. The present paper describes a triple hybrid involving these two genera as well as Zea, and combining in one plant all of the chromosomes from these widely different representatives of the tribe Tripsaceae.

Chromosome Behavior in Zea × Tripsacum Hybrid

The possibility of producing a triple hybrid involving all the chromosomes of Zea, Tripsacum, and Euchlaena, suggested itself immediately when the cytological behavior in the hybrid Zea × Tripsacum was studied. These results have already been mentioned briefly[10] and will be reported in greater detail elsewhere. Suffice to say here that this hybrid, like many other hybrids between distantly related forms, produces gametes with the somatic chromosome number. There is complete lack of pairing between the 10 Zea and the 18 Tripsacum chromosomes, resulting in many and varied irregularities in gametogenesis. Due to the marked lagging of the chromosomes, all of them sometimes become enclosed in a single nuclear membrane. At the second meiotic division these unreduced microspores divide equationally to produce gametes having a complete set of both Tripsacum and Zea chromosomes.

The production of unreduced gametes has been demonstrated by both cytological and genetic results, the latter showing not only that unreduced gametes are produced but indicating that all of the functional gametes may be of this type. The hybrid is completely pollen sterile but is partially fertile when backcrossed by either of its parents, exhibiting a fertility of about 3.4 per cent when crossed with Zea, and 1.3 per cent when crossed with Tripsacum. When a hybrid plant which has received from its Zea parent the gene for yellow endosperm is backcrossed by maize with white endosperm, all of the resulting seeds are yellow, indicating that all functional gametes must receive the chromosome from Zea which bears the gene for yellow endosperm. Since there is no reason for suspecting that this particular chromosome is any more essential to the functioning of the gametes than any other, and may be less so, since its effect on vigor, when in the trisomic condition is less than that of other chromosomes, the natural conclusion must be that this chromosome, and probably all others as well, are included in the functional gametes. The cytological results are in complete agreement with this assumption. All the progeny so far studied from the backcrosses of the hybrid with Zea have



PLANTS OF THE TRIPLE MAIZE HYBRID AND OF ITS PARENTS

Figure 1

The two nearest relatives of maize (*C*) are Tripsacum (*A*) and Euchlaena (*D*). Maize and these two "cousins" are the only two American genera belonging to the tribe Tripsaceae. Maize is quite readily crossed with Euchlaena but viable crosses with Tripsacum have been made only with difficulty. A maize Tripsacum hybrid is shown at *B*. Crosses between Tripsacum and Euchlaena have never been successful. Nevertheless, it has proved to be possible to cross the hybrid (Zea × Tripsacum) with Euchlaena. Such a triple hybrid [(Zea × Tripsacum) × Euchlaena] is shown at *E*. On account of the peculiar cytological behavior of the chromosomes when these hybrids form germ cells, it happens that the triple hybrid has a complete set of the chromosomes of each of the three genera. This triple hybrid is sterile, though there is a *possibility* that a fertile true breeding form might be produced.

38 chromosomes which, since the Zea pollen contributes only 10, must indicate that the hybrid contributes 28, the sum of the chromosome numbers of its two parents.

Introducing the Third Genus

Knowing that the gametes produced by the hybrid Zea × Tripsacum were all, or chiefly, unreduced gametes having one genom of Tripsacum and one genom of Zea chromosomes, it was at once apparent that if the hybrid could be crossed with Euchlaena the resulting progeny would all be triple hybrids and would, furthermore, all be trigenomic, having one genom from each of the three parental genera.

Pollen of Florida teosinte, *Euchlaena mexicana*, was applied to the silks of 208 female florets of the hybrid. Of this number 12, or 5.8 per cent, set seed. This represents a slightly higher percentage of fertility than resulted when corn pollen was applied but the difference is probably of no significance since the latter pollinations were made in the field and the former in the greenhouse under conditions more favorable for successful pollination. There is, however, no evidence that the hybrid is any less fertile with Euchlaena than with either of its parents. Most of the seeds were plump and sound and germinated readily. The resulting progeny was quite uniform, indicating further that the gametes received from the hybrid parent were all identical.

Cytology of Triple Hybrid

The hybrid has 38 somatic chromosomes comprising, presumably, one genom of 10 from Zea, another genom of 10 from Euchlaena, and a third genom of 18 from Tripsacum. The behavior of the chromosomes at meiosis can almost be predicted from our previous knowledge of meiosis in other hybrids involving these genera. It has been shown by Longley[8], Randolph (unpublished), and Beadle[1] that there is almost complete pairing of Zea and Euchlaena chromosomes in hybrids of these two genera, and by Emerson and Beadle[3] that crossing-over between Zea and Euchlaena chromosomes occurs almost, if not quite, as freely as between Zea chromosomes alone. The present writers have shown[10] that in hybrids of Zea and Tripsacum there is little if any pairing of the chromosomes from the two genera. On the basis of these facts we might expect to find meiosis in the hybrid following one of two courses. If the Tripsacum chromosomes are no more closely related to the Euchlaena chromosomes than they are to the Zea chromosomes, we should expect to find complete pairing of the Zea and Euchlaena chromosomes to form 10 bivalents while the 18 Tripsacum chromosomes all behave as univalents. If, however, Euchlaena occupies an intermediate position between Zea and Tripsacum, it is possible that the Tripsacum chromosomes would be homologous, or partially homologous, to those of Euchlaena and we should expect to find some pairing between Tripsacum and Euchlaena chromosomes in addition to the pairing between Euchlaena and Zea chromosomes. Such a situation would probably result in the formation of trivalents, with a reduction in the number of univalents.

Cytological studies show the behavior at meiosis to follow the first course completely. There are usually 10 bivalents during diakenesis and metaphase of the first division and their size indicates that they comprise only the Zea and Euchlaena chromosomes. The lagging univalents are 18 in number and all are small like Tripsacum chromosomes. (See Figure 2A.) Since we are not yet able to distinguish the different chromosomes by morphological details, the question of size is an important one. The Tripsacum chromosomes average much smaller in size at metaphase than the Zea chromosomes, and though it is not always possible to designate any given chromosome as Zea or Tripsacum, the difference in size becomes very evident when metaphase figures of two hybrids, one having two genoms of Tripsacum and one

produced.

of Zea, the other two genoms of Zea and one of Tripsacum, are compared. These are shown in Figure 2, *B* and *C*. When the meiotic figure of the triple hybrid is compared with them, it is readily apparent that the metaphase in the triple hybrid is almost identical to that in the hybrid having two genoms of Zea and one of Tripsacum.

At the anaphase the chromosomes of the bivalents usually separate regularly and pass to the poles while the univalents are distributed at random. Only a few observations on this phenomenon have been made but the fact that one daughter nucleus is often larger than the other indicates that this is the usual procedure.

All of the chromosomes are usually included in the daughter nuclei. Microcytes and micronuclei are seldom found.

The second division shows no irregularities and the only irregularities observed in the microspore tetrads are slight differences in the sizes of the microspores. When differences occur, microspores of approximately equal size always lie side by side in the tetrad and never opposite. This indicates again the random distribution of the chromosomes at the first division and their regular behavior at the second.

The cytological behavior of the hybrid is almost identical to that found in the hybrid produced by backcrossing Zea × Tripsacum with Zea. This hybrid also has 38 chromosomes and at meiosis produces 10 bivalents and 18 univalents. (Figure 2*B*.) The former separate and proceed to the poles quite regularly and the latter go to one pole or the other, apparently at random.

Relationship of the Three Genera

Association of chromosomes must always be interpreted with considerable caution since chromosomes known to be homologous sometimes fail to pair, while others known to be unrelated occasionally become intimately associated. In this case, however, the results are so consistent with our previous knowledge of chromosomal relationship in these genera, and so thoroughly in accord with the taxonomic positions of the genera, that we are probably not far amiss if we conclude that the chromosomes of Zea and Euchlaena are partially, if not completely, homologous, while those of Tripsacum are homologous to neither those of Zea nor Euchlaena. In other words, Zea and Euchlaena appear to be closely related while Tripsacum is not so closely related to either and we have no evidence from our studies that it is more closely related to one than to the other. Collins[2] suggests that if a linear arrangement of the three genera is to be adopted the most reasonable sequence is: Tripsacum, Euchlaena, and Zea. Our cytological observations furnish no evidence either for or against this arrangement which, from the taxonomic and morphological standpoint, is undoubtedly the most logical.

Fertility of the Hybrid

The hybrid proved to be completely male sterile, producing no pollen whatever. Fortunately, at the time that the triple hybrid was in bloom, pollen from all three of the parental genera was available and backcrosses were made on the hybrid with the following results:

Pollen used	No. florets pollinated	No. seed set
Euchlaena	289	0
Zea	104	1
Tripsacum	34	0

The high degree of sterility among the ovules was rather surprising since another hybrid, having two genoms of Zea and one of Tripsacum, and, as already mentioned, a cytological behavior almost identical to that of the triple hybrid, showed a fertility among the ovules of approximately 21 per cent. Judging from the cytological observations, the triple hybrid produces gametes all of which have 10 chromosomes, comprising both Euchlaena and Zea chromatin, and in addition a varying number of Tripsacum chromosomes ranging theoretically from 0 to 18. An appreciable percentage of such ovules might be expected to function with Zea or Euchlaena pollen but apparently they

MEIOSIS OF TRIPLE HYBRID COMPARED WITH MAIZE-TRIPSACUM HYBRIDS
Figure 2

The Zea and Euchlaena chromosomes pair to form ten bivalents, while the eighteen Tripsacum chromosomes behave as univalents (*A*). The size and number of bivalents and univalents is similar to another hybrid (*B*) which has two sets of Zea chromosomes and one of Tripsacum and in marked contrast to a third hybrid (*C*) which has two sets of Tripsacum and one of Zea. Only twelve of the eighteen bivalents are illustrated in the last figure. Magnification 2150×.

do not since only a single seed was produced from several hundred pollinations.

A comparison of the characteristics of the hybrid with its three parents is set forth in Table I. Naturally, it is impossible to make a strictly accurate comparison among the four types of plants involved because their growing season is so different. All that we have attempted to do is to make observations and measurements on the three species and their hybrid when they were at comparable stages of development. Our classification of the characteristics studied as "qualitative" and "quantitative" is purely arbitrary though the former can, in general, be described by observation, the latter only by measurement.

Inheritance of Parental Characters in the Hybrid

Though the hybrid clearly exhibits characteristics of each of its three parents, it shows a greater resemblance to Euchlaena than to either of the other two component genera. This resemblance is so striking that, from the taxonomic standpoint, the hybrid, if it occurred in nature, would probably be classified as a species of Euchlaena. It resembles Euchlaena in all of the qualitative characters considered except one: the presence of secondary branches in the tassel, and approaches this genus in a number of quantitative characters including: number of nerves per cm., number of tillers, percentage of pistillate spikelets in tassel, number of ovules per ear, average length of styles, and number of days from planting to blooming.

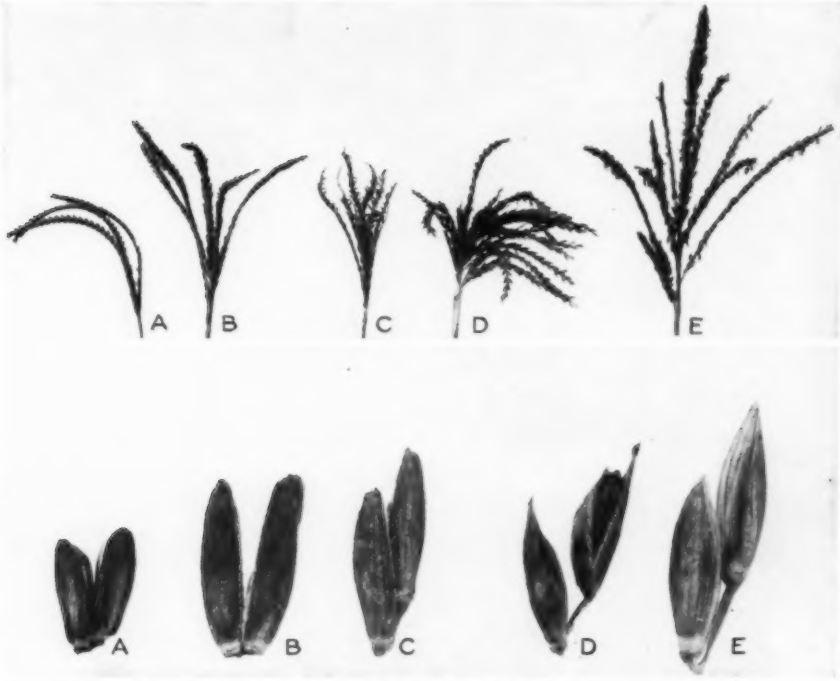
At first glance it might be concluded that the characters of Euchlaena are, for the most part, dominant over those of the other two genera, but further study shows that the hybrid exhibits, in almost every case, the character which is common to two of the three parents. It so happens that every character, among the qualitative characters, which Euchlaena exhibits, except the presence of secondary branches in the tassel, also occurs in one of the other genera. Euchlaena resembles Zea in annual growth habit, absence of root stocks, pedicels on the second male spikelet, bracts or husks enclosing the spike, and branching of lateral inflorescence. Euchlaena resembles Tripsacum in the absence of the central spike in the tassel, number of rows of functional pistillate spikelets, brittleness of the rachis, and an indurated shell consisting of the rachis and outer glume enclosing the seed. Thus in nine of the ten qualitative characters considered,

Euchlaena resembles one of the other genera, as well as the hybrid. The tenth character, absence of secondary branches in the tassel, is common to Zea and Tripsacum but not to Euchlaena, and here the hybrid resembles the first two genera and not the last. All of the qualitative characters, then, exhibit the same type of inheritance shown by flinty and floury endosperm in maize, where two doses of one are always dominant over a single dose of the other. The marked resemblance of the hybrid to Euchlaena may be nothing more than the expression of this type of inheritance.

Though two doses of one character are always dominant to one dose of the other, the dominance is by no means complete and the influence of the "recessive" parent is usually apparent in the hybrid. Though the hybrid, like Zea and Euchlaena, is an annual, it has a weak perennial tendency; the ears are enclosed in husks, but these are often too short to cover the entire spike; one of the male spikelets is pedicelled but the pedicel is much shorter than that of either pedicelled parent. And, though the hybrid resembles Euchlaena and Tripsacum in having a brittle rachis, it is one which disarticulates less readily than that of these two genera; the seed is enclosed in an indurated shell but this structure is less horny than that of Tripsacum and Euchlaena and its glumes are more prominent and the rachis less a conspicuous part. In fact, the only characters which exhibit a clear-cut dominance when two doses occur are the absence of root stocks and the absence of the central spike in the tassel.

When we consider the quantitative characters we see that they are inherited in precisely the same way except that the dominance of a condition received from two of the three parents is not quite so clear-cut. The hybrid resembles Euchlaena and Zea in having wide leaves, few nerves per unit of width, few pistillate spikelets in the tassel, and in having the bipartite style fused most of its length; it resembles Euchlaena and Tripsacum in having numerous tillers, many ears, few ovules per ear, and a long period from planting to blooming; it resembles Zea and Tripsacum in having a relatively small number of staminate florets. In these characters, as with the qualitative characters discussed previously, the influence of the third genus is usually apparent. The presence of pistillate spikelets in the tassel is a good example of this. Neither Zea nor Euchlaena normally have pistillate spikelets in the tassel, though in some genetic types this condition occurs regularly and it may also be induced in almost any variety by abnormal growing conditions. Tripsacum, on the other hand, always has pistillate spikelets in the terminal inflorescence. In our Tripsacum the ratio of staminate to pistillate spikelets is 15.2:1. Weatherwax[14] reports a ratio of 18.5:1 in his stock. In the triple hybrid the ratio is 239:1.

In characters in which the three genera are all different, the condition in the hybrid approaches the average of the three parents. In length of styles, for example, the parents are 233 mm., 76 mm., and 14 mm., with an average of 108 mm. The average length of styles in the hybrid is 99 mm. When two of the parents are rather closely alike, however, the hybrid seems to approach the condition of the two similar parents more closely than it approaches the average of all three. Number of seeds per spike is a good example of this phenomenon. Euchlaena and Tripsacum are both low, with 5.7 and 9.6 ovules, respectively. The variety of Zea used in this hybrid has an average of 485 ovules per spike. The average of the three parents is 167 ovules. The average of the hybrid is 14.2, which approaches Tripsacum and Euchlaena much more closely than it does the average of all three. The same situation holds true for width of leaves, number of veins per cm., percentage of length that the styles are fused, percentage of pistillate spikelets in the tassel, and number of days from planting to blooming. In other words, there



TASSELS AND MALE SPIKELETS OF PARENTS AND HYBRIDS

Figure 3

The tassels and spikelets of the four types are arranged in the same order in the two groups. Tripsacum (*A*), Zea × Tripsacum (*B*), triple hybrid (*C*), Euchlaena (*D*), and Zea (*E*). The central spike characteristic of Zea is absent in Tripsacum, Euchlaena, and in the triple hybrid. The staminate spikelet of the triple hybrid (*C*) is pedicelled, an evidence of the influence of Zea and Euchlaena.

is a decided indication in both qualitative and quantitative characters that the dominance of two doses is more than a mere additive effect; that two doses are more than twice as effective as one. A similar situation has been observed in some of our Zea × Tripsacum hybrids having different proportions of germplasm from the two parents, and it may be a general phenomenon. There is a further possibility that the marked dominance of two doses is due to the fact that a character common to two of the genera is likely to represent the original or "wild" condition while the contrasting character in the third genus has come about by mutations, most of which are recessive. This possibility is discussed in greater detail in succeeding paragraphs.

Phyletic Significance

Does this trigeneric hybrid of Zea, Tripsacum, and Euchlaena give us any hint as to the botanical nature of the ancestral form from which maize and the other American Tripsaceae have originated? Darwin attached considerable phyletic importance to the reversions resulting from hybridization. Later, when these reversions, as in the case of the blue plumage of pigeons, were explained on a Mendelian basis, their importance as phyletic evidence was

minimized. While we have no desire to revive Darwin's theories on hybridization and reversions, and still less desire to present, at this time, any new theories regarding the origin of maize, when the archaeological, genetic, and cytological evidence bearing on this question is still so meager, and the evidence from taxonomic and morphological studies has already been thoroughly discussed by Collins, Kempton, Weatherwax, and others, yet it may not be amiss to call attention to a few pertinent facts in connection with the triple hybrid.

It is obvious that hybrids of species descending from a common ancestor should show ancestral reversion to the extent that recessive mutations which have occurred in one species are "covered" in the hybrid by non-mutated genes in the other species. This type of reversion occurs daily when laboratory races of Drosophila are crossed, usually reproducing the wild type in the first generation. When all the species which have descended from a common ancestor are recombined, reversion of this type should find its maximum expression. To what extent, in our triple hybrid, the three component genera complement each other to reproduce the ancestral condition, we have no way of determining. Neither can we tell the extent to which any reversionary tendencies may be modified by the differing proportions of germplasm which each of the three genera contributes. If one of them is a tetraploid, as it may be in the case of Tripsacum, its germplasm would have an excessive share in determining the characteristics of the hybrid.

Though the question of the resemblance of the triple hybrid to the ancestral form is nothing more than a matter for speculation, it is of interest and perhaps of some importance to note that we have in this hybrid a plant with such characteristics as might well have existed in the progenitor of the American Tripsaceae.* There is no denying that a plant of this type could have given rise, through mutation and selection, natural and artificial, to Zea, Euchlaena, and Tripsacum. In fact, the potentialities of all three genera already exist in the hybrid, and were it fertile and capable of orderly segregation, it would be theoretically possible to isolate from the progeny of this plant all of the American genera of Tripsaceae which exist today. Furthermore, the plant is one which could probably survive under natural conditions and still constitute promising material for domestication. It is at least as well suited to survival in nature as is Euchlaena, which exists in a wild state in Mexico and Guatemala. The indurated rachis and glumes would protect the seeds from destruction by birds and insects while the partially brittle rachis and the small ears would permit the seeds to become widely scattered. On the other hand, the plant has greater potentialities as a food plant than either Euchlaena or Tripsacum. Collins[2], in considering Harshberger's hypothesis that maize arose from Euchlaena by human selection and recrossing with Euchlaena, states:

> Any plant with the characters of *Euchlaena* would be most unpromising material from which to develop a food plant. As a starting point for selection in the direct line it would seem that we must go back to a plant that had not developed the indurated rachis that encloses the small seeds in both Euchlaena and Tripsacum.

These objections are partly overcome if it is assumed that the ancestor of maize was similar to the triple hybrid. It is true that the seeds are enclosed in a shell but this structure is less horny than that of Euchlaena or Trip-

* Since the above was written we have received a paper by Weatherwax in which he describes, on the basis of morphological studies, the probable nature of the progenitor of maize. It is interesting to note that his description, with a few exceptions, is very similar to a description of the triple hybrid. See: WEATHERWAX, PAUL; The Phylogeny of Zea Mays. *Amer. Midland Naturalist*, 16:1-71, 1935.

EARS OF PARENT AND HYBRID

Figure 4

Pistillate spikes of Zea (*A*), Tripsacum (*B*), Euchlaena (*C*), Zea × Tripsacum (*D*), triple hybrid (*E*). While the triple hybrid contains a complete set of ten maize chromosomes, the maize characteristics are almost completely suppressed in the hybrid ear.

sacum. Also, the seeds, judging from the single one so far obtained, would be much larger than those of Tripsacum and Euchlaena, being as large, in fact, as some of the smaller-seeded varieties of maize in existence today. On the whole, the plant would be scarcely less promising as material for domestication than some of the varieties of Coix which are grown in the Orient today.

Other Triple Hybrids

Complex hybrids involving three, or

even more, species are not uncommon. Renner[12] mentions a number of hybrids combining three or more species and some of the vegetatively propagated horticultural plants, such as varieties of Vitis, Rubus, and Rosa, have very complex pedigrees including several species in their ancestry. There must be made, however, a clear distinction between triple hybrids which merely involve three species in their pedigree and those which, through cytological and genetic studies, are shown to combine all the chromosomes of the three parental species. The former, because of segregation, may include little, if any, of the germplasm of some of the species in the pedigree while the latter must combine all the germplasm of the three component species. Hybrids of this kind are *trigenomic* since they possess one genom from each of the three parents. Of the recorded cases of triple hybrids which are also trigenomic, only one, besides the triple hybrid of Zea, Euchlaena, and Tripsacum, involves three distinct genera. This is the hybrid of Aegilops, Triticum, and Secale, described by Tschermak and Bleier[13], and later by Leighty and Sando[7]. Neither of these papers presents cytological evidence of a trigenomic condition but from the known behavior of the Aegilops × Triticum hybrid in producing unreduced gametes, it may be assumed that this hybrid is of such a nature.

Trigenomic hybrids involving three distinct species are more numerous but by no means common. Kostoff[5] has reported a Nicotiana hybrid which he designates as *Nicotiana triplus,* combining the species *N. tabacum, N. sylvestris* and *N. rusbyi.* This hybrid is completely fertile and the cytological behavior quite regular. Apparently 12 of the *tabacum* chromosomes pair with the 12 *sylvestris* chromosomes, while the remaining 12 *tabacum* chromosomes pair with 12 *rusbyi* chromosomes. Kostoff[6] also reports a trigenomic hybrid of Triticum, combining the chromosomes of *T. dicoccum, T. monoccum,* and *T. vulgare.* This hybrid is only partially fertile. Karpechenko[4] has produced a number of triple hybrids of different species of the Cruciferae. He has crossed Raphanobrassica, a fertile

VARIATION IN LENGTH OF SILK

Figure 5

The styles of Zea (*A*), Euchlaena (*B*), Tripsacum (*C*), Zea × Tripsacum (*D*), and of the triple hybrid (*E*). The silks of the hybrid are fused most of their length as in Zea and Euchlaena, but the influence of Tripsacum is shown in the split at the end. In length of silks, the hybrid much more closely resembles Zea and Euchlaena than Tripsacum.

tetraploid hybrid of *Raphanus sativa,* the common radish, and *Brassica oleoracea,* ordinary cabbage, with other species of the Cruciferae and has obtained hybrids of Raphanobrassica with Abyssinian mustard, *Brassica carinata;* rape, *Brassica napus;* horse radish, *Brassica raphanistrum;* chinese cabbage, *Brassica pekinensis;* and the turnip, *Brassica campestris.* Cytological investigations have shown all the hybrids to be trigenomic. Some of the hybrids are partially fertile and from these Karpechenko expects to obtain true-breeding triple hybrids.

There seems little chance of obtaining a fertile and constant triple hybrid of Zea, Tripsacum, and Euchlaena unless a doubling of the chromosomes should take place in vegetative tissue. The behavior of the chromosomes at meiosis is such that it practically precludes the formation of unreduced gametes, and even if they were produced, the failure of the anthers to dehisce would prevent them from being available for pollination. A fertile, true-breeding, triple hybrid might be produced by first developing a fertile hybrid of Zea and Tripsacum by crossing tetraploid Zea and tetraploid Tripsacum, doubling the chromosome number of this hybrid by Randolph's[11] method of heat treatment, and crossing this octoploid hybrid with tetraploid Euchlaena. Since such a hybrid would be of chief interest only as a curiosity and would have less genetic and cytological value than the sterile triple hybrid already available, it seems scarcely worth while to attempt to produce it.

The chief value of triple hybrids is in permitting a direct cytological study of chromosome relationship, measurement of the combined effects of different types of germplasm, and in "bridging the gap" between two genera or species which cannot otherwise be crossed.

Summary

1. Cytological and genetic studies of the hybrid Zea × Tripsacum indicate that it produces only unreduced gametes having the somatic chromosome number.

2. By crossing this hybrid with Euchlaena a triple hybrid, having a complete chromosome complement from each of the three genera, is produced.

3. At the meiotic division in the triple hybrid there is complete pairing of ten Zea chromosomes with ten Euchlaena chromosomes with all the Tripsacum chromosomes behaving as lagging univalents.

4. The hybrid exhibits, in almost every case, any character which is common to two of the three genera, two doses of a condition being usually dominant to one dose of the alternative condition.

Table I. Characteristics of three genera of Tripsaceae and their triple hybrid.

Character	Zea	Euchlaena	Tripsacum	Triple hybrid
Growth habit	Annual	Annual	Perennial	Annual
Root stocks	Absent	Absent	Present	Absent
Central spike in tassel	Present	Absent	Absent	Absent
Secondary tassel branches	Absent	Present	Absent	Absent
Pedicells on second male spikelet	Pedicelled	Pedicelled	Sessile	Pedicelled
Female spike enclosed in husks	Enclosed	Enclosed	Naked	Enclosed
Branching of lateral inflorescence	Present	Present	Absent	Present
No. rows functional pistillate spikelets	Many	Two	Two	Two
Brittleness of rachis	Solid	Brittle	Brittle	Brittle
Seeds enclosed in shell	Naked	Enclosed	Enclosed	Enclosed
Average No. tillers	0.1	6.5	19.0	6.0
Average width of leaves, cm.	5.4	4.8	1.0	6.0
Average No. nerves per cm.	3.5	4.2	8.1	4.0
Average No. branches per tassel	14.4	18.9	3.0	6.4
Average No. staminate florets in tassel	462.0	1512.0	274.0	334.0
Average No. pistillate florets in tassel	0.0	0.0	18.0	1.4
Per cent pistillate florets in tassel	0.0	0.0	6.6	0.4
Average No. ears	1.8	165.0	95.0	41.0
Average No. ovules per ear	485.0	5.7	9.6	14.2
Average length of styles, mm.	233.0	76.0	14.0	99.0
Percentage of length styles are fused	99	99	0.0	94.9
Days, planting to blooming	95.0	210.0	210.0	192.0

5. Certain characteristics of the hybrid may perhaps be regarded as of phyletic importance.

6. The genetic and cytological importance of complex hybrids is discussed.

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Criminality in Twins

At a meeting of the Deutsche Gesellschaft für Vererbungswissenschaft, Dr. Heinrich Kranz, of the Kaiser Wilhelm Institut für Anthropologie, menschliche Erblehre und Eugenik, announced the results of further research in criminality in twins. The examinees were inmates of the Prussian prisons. Up to the present time, twenty-seven enzygotic and thirty-seven dizygotic twins have been studied. In seventeen of the enzygotic groups, both twins had received a sentence for a crime or misdemeanor; in ten of the groups only one of the twins had incurred a penalty. Agreement, or concordance, was evidenced in 63 per cent, and differentiation, or discordance, in 37 per cent. In eighteen dizygotic groups, both twins had received a sentence; in nineteen groups, only one twin (46 per cent and 54 per cent, respectively). The agreement, or concordance, does not run as high as in the researches of J. Lange and of Legras. In the penalized groups of twins the enzygotic groups reveal great similarity in the number of penalties incurred and as to the time when the first penalty was imposed, but less similarity in the severity of the penalties and in the nature of the crimes and misdemeanors. The dizygotic groups show, on the other hand, marked differences in all these points. In the groups composed of a male and a female, the differences between the enzygotic and the dizygotic groups were less marked. The hereditary influence is therefore strongest with reference to the repetition of the crimes, and next with regard to the time of onset of the criminal conduct. The severity of the penalties and the type of crime committed depend more on environmental influences. Combining the results secured by J. Lange, Legras and Kranz in their examination of twin groups with respect to criminality, one finds thirty enzygotic twin groups concordant and thirteen discordant (70 and 30 per cent, respectively); twenty dizygotic twin groups concordant and thirty-nine discordant (34 and 66 per cent, respectively). A deeper perception of the differences and the similarities in the two groups will be secured when a detailed examination of the individuals has been made.

Journal of the American Medical Association

FIVE GENERATIONS OF POLYDACTYLISM

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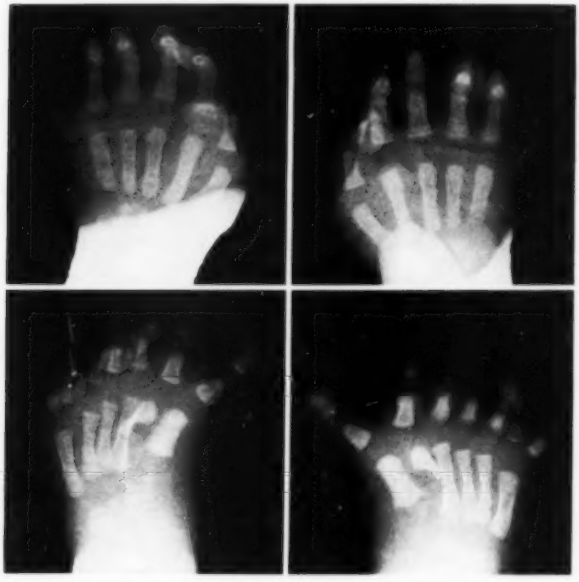


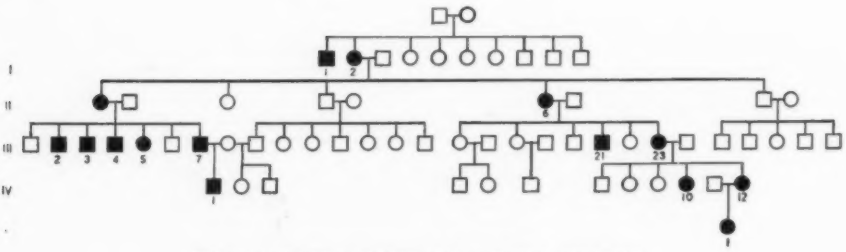
SIX FINGERS AND SEVEN TOES
Figure 6

X-ray photograph of hands and feet of baby discussed in this article. There are six fingers on each hand and seven toes on each foot. The ring and little fingers of each hand are webbed but there is no webbing between the toes.

POLYDACTLYISM is the occurrence of supernumerary digits on either the hands or feet. For a long time it has been recognized as a hereditary defect. It is not a rare condition and numerous cases have been reported in medical and other scientific journals but there are not many reports showing the line of descent, due probably to the lack of family records.

Syndactylism is the occurrence of webbed fingers and toes. It is also a hereditary condition and may or may not occur in conjunction with polydactylism.[3] It is considered to be a dominant trait.[2] The Lawrence-Biedl syndrome, consisting of adiposogenital dystrophy, retinitis pigmentosa and mental deficiency, and often including polydactyly, is believed to be a genotypic inherited unit character defect because the different symptoms are all individually inheritable.[4]

Brandeis reported a polydactyl family in which the condition seemed to act as an irregular dominant.[1] Snyder reported a large family of Negroes in an isolated district, with records of 171 individuals of whom 54 had extra fingers and toes.[7] There were several cases of mating between polydactylous people.



FIVE GENERATIONS OF EXTRA DIGITS

Figure 7

Pedigree chart showing the inheritance of polydactyly in the family described in the accompanying text. The direct ancestry of the propositus (*V-1*) might suggest maternal inheritance as the character has been transmitted from mother to daughter for five generations but the preponderance of females is probably a chance deviation.

He concluded that the defect was a recessive trait.

Punnett and Pease believe there is a definite factor for polydactylism.[6] They reported on the condition in chickens in which the gene was carried by apparently normal four-toed birds. They explained the defect's non-appearance in certain fowls by the presence of a factor which inhibited the action of the determiner for polydactylism.

Case Report

On June 10, 1934, a four months old girl baby was admitted to the Station Hospital, Fort Sheridan, Ill., for amputation of extra fingers and toes. The baby was illegitimate, the father had deserted before the child was born, the mother had a hare lip and cleft palate which made her speech difficult to understand.

The baby had six fingers on each hand and seven toes on each foot. Thumbs and two adjoining fingers were normal, the ring and little fingers of each hand were webbed in their full length. The sixth or extra finger was loosely attached at the base of the normal little finger on each hand. X-ray (Figure 6) showed two phalanges in each thumb, three in each of the other fingers. There were five normal metacarpal bones, none corresponding to the sixth finger.

None of the toes was webbed. The feet were broader than normal. The inner two digits of each foot were big toes in appearance, with two phalanges, as confirmed by X-ray (Figure 6). The other five toes had three phalanges, rudimentary in the seventh however. There were five metatarsals normally formed, and an extra rudimentary metatarsal between the first and second, and in line with the second great toe. There was no difference between either hand or either foot. In all other respects the baby was healthy and well formed with no visceral or other bony defects.

The operation was performed June 11, 1934. The extra fingers were removed and the web between ring and little fingers separated and repaired. Only the great toe on each foot was removed, as the family would not consent to the amputation of two toes. Recovery was rapid, convalescence uneventful. On October 1, 1934, the baby appeared to be developing normally.

Family History

The patient, *V-1* in Figure 7, was the fifth individual in the direct maternal line to show polydactylism. Besides the mother, both the grandmother and the great grandmother of the baby were living in a nearby village. The great grandmother, *II-6* in the family tree, her sister, *II-1*, and their brother, *II-4*, were visited. From them the details of the family history were learned. Their mother *I-2*, now dead, had emigrated to the United States from Alsace. She told her children that she

EXTRA TOES

Figure 8

Feet of the mother of the baby whose hands and feet are shown in Figure 6. Note that two big toes are present, one of them having two phalanges as in the normal big toe. In this family the polydactylism is inherited in the maternal line for five generations.

had had a brother with extra fingers and toes who died in infancy, as well as seven normal brothers and sisters. The mother also told them that she was the first member of the family to show polydactylism as her father and mother had never heard of the defect until it appeared in two of their children.

In other respects the family seemed normal. They were ordinary Americans with surnames of British and German origin. Careful questioning revealed no evidence of hereditary diseases. No members of the family were outstanding, none had risen above the laboring class economically, but none were paupers. The hare-lip of *IV-12*, the mother of the baby on whom we operated, was the only defect besides the polydactyly and syndactyly. None of the family was feebleminded, nor was there any blindness or obesity.

A study of the family tree (Figure 7) shows certain facts. All polydactyl members of this family have a parent who is polydactyl except *I-1* and *I-2*. The defect does not skip any generations. Every polydactyl person who has had issue has produced one or more children with extra fingers and toes. No normal individuals, though sprung from a polydactyl parent, have any descendents who are affected; so far, once free of the defect, each line has remained free. There are no known consanguineous matings.

The defect was transmitted on the maternal side except in the case of *III-7* who passed it on to his son. The character is not considered to be sex linked as there has been rather a large infant mortality among the boys. *III-7*

is the only male who has reached maturity and reproduced.

An interesting example of the transmission of the polydactyl character occurred. *III-9,* free of the defect and presumably a recessive, married and reproduced two normal children. He then died and his widow married *III-7,* a polydactyl who was first cousin to her deceased husband. The result of this union was a polydactyl child, *IV-1.*

Examination of Different Members

Of the fifteen polydactyl members of this family, ten were examined by us personally, the other five are dead. The usual arrangement of digits was six fingers on each hand and seven toes on each foot. However, three individuals had six toes on one foot and seven on the other; one had six toes on each foot. *III-7,* in addition, had double terminal phalanges in each thumb, the soft parts webbed. He demonstrated great strength in these thumbs and considered them an asset in his work as a machinist. All of these individuals had had the sixth fingers amputated, but except in the case of *IV-12,* they still had their extra toes intact. The scars of amputation were visible in all and in some cases X-ray showed spur formation at the site of amputation.

Figure 8 is a roentgenogram of the feet of *IV-12,* mother of our original patient. Six metatarsal bones are seen, the second defective at the proximal end. The first two digits are big toes with only two phalanges. The proximal head of the sixth toe remains from a former amputation. The feet are symmetrical.

As for syndactylism, we observed either webbed fingers or toes in five members of the family and found it absent in five polydactyls. *I-2* was believed by her children to have had some webbed toes. The living members were uncertain in their minds about webbing in the four other dead polydactyls. Syndactylism did not occur in the absence of polydactylism. No conclusions can be drawn as to syndactylism in this family as the data concerning the appearance of this defect are incomplete.

Conclusions

A family is described in which extra fingers and toes are present in five generations. We believe that polydactylism, in this family at least, is a dominant Mendelian character. If we were to assume that it was recessive, we would also have to assume that six different individuals in this group who were recessive found mates who were heterozygous for this character. This would be most unlikely in the absence of consanguineous mating.

If, however, we assume the character under discussion to be a dominant we find it fulfills the requirements for dominance very well. It occurs in every generation. It shows up, on the average, in about half of the offspring. Thus, of six matings where one parent was polydactyl, there were thirteen children with extra fingers and toes and twelve normal children. Every polydactyl parent has transmitted the character to some of his offspring. All matings where both parents were normal have produced only normal children.

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CHINCHILLA MUTATION IN THE WILD HARE

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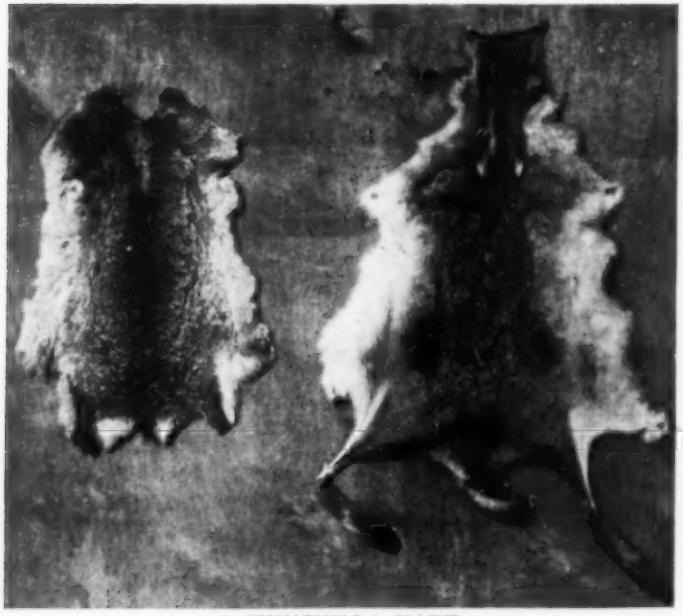

A CHINCHILLA HARE
Figure 9

On the left is shown the pelt of a chinchilla rabbit; on the right that of the chinchilla hare shot near Krakow. The chinchilla pattern in the rabbit is a well known variation conditioned by an allelomorph of the normal pigmentation gene which results in hair pigmentation lacking yellow. Nothing is known about the inheritance of the chinchilla pattern in the hare but in appearance it is a striking parallel to the pattern in the rabbit.

ON October 27, 1934, a very interesting specimen of the wild hare (*Lepus europaeus*) was shot in the fields of the Experimental Stations of the Jagellonian University, about three miles from Krakow. At first the huntsmen thought that it was a rabbit, although its dimensions and particularly its long hind legs, as well as the general conformation of the animal, showed the peculiarities of the hare without any question.

The character of the coat, however, was most striking, in that it closely resembled that of the so-called chinchilla rabbit, well known for its valuable pelt. As it is possible to see from the photograph (Figure 9), the coat of this hare consisted almost entirely of uniform, fairly fine, hair with sparsely distributed, coarse, white, single hairs. Yellow pigment was entirely lacking, as is the case with the real chinchilla coat. The hair is perhaps a little longer than in the chinchilla rabbit, and will be studied to elucidate its peculiarities.

The hare, a female, also seemed nor-

mal in regard to the proportions of the bones and in body weight.

In view of the recessive nature of the chinchilla coat in the rabbit it is not impossible that such a specimen could be met among the wild hares in the neighboring fields, but till now none has been shot having a chinchilla coat. This case presents a good example of a parallel mutation occurring in closely related species and subspecies.

I wish to thank Prof. T. Marchlewski for permission to make use of the coat of chinchilla rabbit from the museum of genetics for comparison (Figure 9). My thanks are also due my assistant Dr. B. Slizynski for the accompanying photograph.

A Monoecious Date Palm

ON page 113 of *Date Growing in the Old and New Worlds* by Paul B. Popenoe, the statement is made "that in all parts of the world monoecious date palms are occasionally found—that is, palms on which one cluster will be composed of male flowers, and another of female flowers." Although not so stated, it is inferred from further comment in this same source that either a male or a female may develop the characters of the opposite sex. In October of this year (1934) Prof. D. W. Albert of the Department of Horticulture of the University of Arizona, called the writer's attention to a monoecious palm located in the University of Arizona Date Garden near Tempe, Arizona. When the flowers of this palm first appeared in 1931, it appeared to be a normal male, and the abundance and viability of the pollen were recorded as "fair," although no pollinations nor germination tests were made. This year the pollen was rather sparse and apparently very low in viability. Two flower bunches developed a light setting of fruit, as shown in the accompanying photograph. At the time of examination the fruit had not ripened but a few of the seeds were examined and Prof. Albert states that the seeds have a well developed germ pore and are of normal size.

A BISEXUAL DATE PALM

Figure 10

The male inflorescence above bears no fruits, but the one below it, bearing many nearly mature fruits, is obviously of the opposite sex.

Three other monoecious palms have been authentically reported to the writer, and they also were originally males. The monoecious character is unstable and of no economic value, although it is of considerable interest to the plant breeder in that it may throw some light on the mechanism of sex determination in this species, particularly in connection with a study of the chromosomes. It is hoped that others who observe these monoecious palms will report them.

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MEDICO-GENETICS

A Review

ON three afternoons during the autumn of 1933, record crowds composed mainly of faculty and students swarmed into "Amphitheater C" at the Harvard Medical School to hear Dr. Otto L. Mohr deliver his addresses upon "Genetics and Pathology." They filled every available seat; they sat on the steps; they lined the aisle above; they stood in the doorways. No previous Dunham Lecturer had been greeted by so large an audience. These interested Harvard crowds constituted not only a tribute to the lecturer himself but were highly indicative of the interest which is now beginning to be mainfested in Medical Schools with regard to the application of genetic principles to the study of medical problems.

The material of these lectures has now become the basis of a book* which, under the title of "Heredity and Disease," is easily the most outstanding popular presentation of the subject today in the field of Medico-genetics. The book is divided into a preface, five chapters, a group of half-tone plates, a list of general works on heredity, and an index.

Chapter I introduces the reader to hereditary factors, personal characters, and the relationship between the two; how gametes link generations and how each hereditary character, normal or abnormal, is determined by one or more of the hereditary units, the genes. The phænotype, or end product, is a balance resulting from equilibrium between environment and genotype. Alter either, and you alter the phænotype. For example, onychoryphosis (hypertrophy of nails) is inherited, but manifests itself only in the feet of persons who wear shoes.

Chapter II reviews the mechanism of cell division and the detailed behavior of chromosomes in mitosis, their reduction to the haploid number at maturation, and their restoration to the diploid number at subsequent fertilization. Whether a zygote is to be female or male depends upon whether the fertilizing sperm carries an *X*-chromosome or a *Y*-chromosome. It is impossible to change the sex ratio in man, and the best we may expect to do is "to influence somewhat the probability of obtaining one sex in preference to the other."

Mendelism

In Chapter III Mohr retells the story of Mendel's discovery of the laws of heredity and his supreme disappointment at having it rejected by all to whom he sent his manuscripts; then the dramatic rediscovery by De Vries, Correns, and Tschermak; then the first application of Mendelism to man by Farabee, working on shortened fingers or brachydactyly. There follows mention of the brilliant demonstration by Sutton that "our knowledge of the distribution of chromosomes provides us with an adequate mechanism for explaining the marvelous numerical constancy of the Mendelian law of inheritance."

We read of the dominance of one of a pair of contrasted characters in the F_1, and of the segregation of genes in germ cells of the F_1, whose random recombination in zygotes of the F_2 results in the 3:1 ratio. An individual may carry a particular gene in double or in single dose, according to whether it was received from both parents or from only one.

"Some dominant genes are so constant in their manifestation that they always strike through." "A great many are so variable in their somatic effects that numerous heterzoygous individuals are perfectly normal." It is impossible to predict from the appearance of the heterozygote what the homozygote will

*Mohr, Otto L., *Heredity and Disease.* Price, $3.50. W. W. Norton, 1934.

look like. Whereas the heterozygote for a dominant gene may manifest a trifling malformation, "the homozygote may bear a far more pronounced and eventually deleterious character." "It is desirable to advise against intermarriage, in general, within families in which dominant malformations occur." Here Peacock's handless-footless Brazilian family is cited. Inherited dominant malformations may become valuable in the medico-legal field where there is a question of parentage.

Consanguineous marriages favor the appearance of recessive traits such as albinism. There is a statistical error introduced in the F_2 data because matings between two heterozygotes are recorded only when they have already produced a homozygous recessive individual. But corrections for this error have been devised by numerous authors.

Inheritance of "white-eye" in Drosophila is used to illustrate the sex-linked mode of inheritance. Sex-linked characters in man include haemophilia, night-blindness with myopia, Leber's optic atrophy, Gower's pseudo-hypertrophic muscular paralysis, and red-green color-blindness. Females exhibiting sex-linked characters may be produced when an affected man marries a carrier.

Humans exaggerate and minimize in relating their family histories. They can not be experimented upon as laboratory animals may. For these reasons and others we can not hope to detect new genetic principles by the study of human material. "The only accessible way to make progress in human genetics is an indirect one. The general laws of heredity must be unveiled by investigations with experimental material, plants and animals, and the interpretation of the carefully collected data on hereditary characters in man must in every case rest upon the comparison with analogous evidence from experimental genetics."

Chromosomes

There follows the explanation of the dihybrid 9:3:3:1 ratio as a combination of two 3:1 ratios. Linkage, or the tendency for certain characters to be inherited together, is due to residence of their determining genes in the same chromosome. The number of linkage groups corresponds to the number of pairs of chromosomes in all adequately studied materials.

Proof of the chromosome theory was first given by Bridges, who studied non-disjunction of the *X*-chromosome in exceptional white-eyed female Drosophilas. These females were predicted from genetic tests to have two *X*-chromosomes and a *Y*-chromosome, which was then shown to be the case cytologically. Sex-mosaics in which one *X*-chromosome had perished in the formation of one of the two daughter cells resulting from the first division of the female zygote were male on the side that lost the *X*-chromosome and exhibited all recessive sex-linked characters for which the 2*X* side was heterozygous. From these studies the principle was established by Morgan and Bridges that each particular cell is self-determining; i. e., the somatic characters of each cell are a direct expression of its own chromosome and gene equipment.

Mrs. Morgan's female Drosophilas with permanently attached yellow-bearing *X*-chromosomes plus a *Y*-chromosome, when crossed to normal gray males, produced a race of such yellow females and normal gray males, because the other expected classes of progeny are non-viable. This may explain a curious human case of mother-to-daughter inheritance of presumably ordinary color-blindness, which case may possibly be examined by means of tissue culture methods.

Genes

A gene may produce a single localized effect, as in ptosis (drooping lids) or alopecia (hairlessness), or it may produce manifold changes. Amaurotic family idiocy shows progressive mental impairment, muscular weakness leading to paralysis, and diminution of vision leading to blindness. Blue sclerotics

is associated with brittle bones, dental anomalies, and in later years with otosclerosis leading to deafness. Cleidocranial dysostosis produces striking skull abnormalities, rudimentary collar bones, defective teeth, and frequently underdevelopment of subcutaneous fat.

As shown by Saller's diagrams:

1. A gene may produce one manifestation.
2. A gene may produce several manifestations.
3. Many genes combined may produce one manifestation.
4. A gene may modify the action of another gene in producing a manifestation.
5. Many genes may modify the action of a gene in producing a manifestation.
6. Genotypical balance is due to interaction of genes in producing the phænotype.

There are point mutations, section mutations, chromosome mutations, and somatic mutations. The latter are exemplified by pied iris in man. The rate of crossing-over, or breakage and exchange of homologous parts between members of a pair of chromosomes, when tagged by known genes, provides a tool whereby we are able to measure chromosomes genetically, distances being proportional to percentage of crossing-over. That physical crossing-over does actually take place has been proven by Stern for Drosophila and by Creighton and McClintock for maize by experiments involving markers in two chromosome partners which, owing to sectional aberrations, were visibly different.

Combined genetic and cytological methods enabled Muller and Painter, and Dobzhansky to construct actual metrical chromosome maps for Drosophila. Heitz and Painter, by differential staining, have been able to study differences in segments, and from visible landmarks Painter has been able to plot actual locations of certain genes. Each normal character depends for its development upon the normal coöperation of many different genes.

Some genes are more apt to mutate than others. Some genes have a large series of alternative forms to which they may mutate, only two of which genes may be present in a single individual. Landsteiner's blood groups are produced by members of such an allelomorphic series, as are the *M* and *N* blood groups of Landsteiner and Levine. By means of these blood groups we can not pick out a particular man as the parent of a child, but we can say to what group or groups he must belong. As yet the blood groups have not been found linked with any other character, but linkage has been shown to occur in man between hemophilia and color-blindness in a pedigree published by Madlener.

Inherited Defects

Chapter IV deals with a number of special topics. Ophthalmology reveals the following hereditary characters: microphthalmus, Coloboma iridis, cataract, Luxatio lentis, aniridia, macular degeneration, retinitis pigmentosa, optic atrophy, night blindness, and red-green blindness of several types, glaucoma, hydrophthalmus, albinism, blue sclerotics, Luxatio lentis associated with arachnodactyly (spider-fingers).

Neuropathology contributes progressive muscular dystrophy, neurospinal dystrophies, spastic spinal paralysis with paraplagia, spinal ataxia, Huntington's chorea, hepato-lenticular degeneration in which both liver and basal ganglia of the brain degenerate.

Otosclerosis and harelip are inherited.

Among the heritable metabolic derangements we find diabetes mellitus, orthoglycæmic glycosuria, diabetes insipidus, alcaptonuria, hematoporphyrinuria, cystinuria, haemorrhagic nephritis, hemolytic jaundice. A clear-cut dominant is angioneurotic œdema.

Attacks are produced in persons who have inherited an allergic hypersensitivity as a reaction to external stimuli. Inherited immunity to *Bacillus suisepticus* in swine is associated with the wild color of the coat.

Other hereditary characters in man are known to dermatology, otology, orthopedics, and dentistry.

Lethal genes are described in Drosophila and in man in which ichthyosis is a good example. Sub-lethals in man

include Xeroderma pigmentum, amaurotic family idiocy, glioma retinæ, spinal progressive muscular paralysis, and osteogenesis imperfecta (brittle bones). "That numerous factors may have a lethal effect is not surprising. What is *really* astonishing is the fact that the coöperation of this multitude of genes is generally so perfect that a very complicated embryological development of the interlocking physiological processes takes a *normal* course, so that as a rule normal, viable individuals are produced."

In identical twins usually neither or both will tend to develop rare hereditary characters. In fraternal twins only one will tend to develop them. In identical twins have been found such characters as complete absence of one leg, cerrathosis pilaris, time of dentition, type of implantation of teeth, and disposition to decay, myopia, hypermetropia, luxatiocoxæ, harelip, goitre, schizophrenia, manic depressive insanity, predisposition to tuberculosis, surgical tuberculosis of the heel bone.

Sex is not a function of the sex-chromosome alone, but a matter of correct quantitative balance between numbers of male- and female-determining genes. Drosophila and Lymantria are discussed as regards sex determination. Each sex possesses the potentialities of the other because each can become intersexual. Intersexes are mosaics in time in that the degree of intersexuality depends upon how early the switch-over occurred. This is true of higher animals as exemplified by the free-martins studied by Lillie and by Tandler and Keller. Higher animals are thus hermaphroditic at fertilization. There follows mention of inherited intersexuality in man, hypospadias in man, and the dramatic story of Crew's Buff-Orpington hen.

Calculations by Morgan, Muller, Gowen and Gay give estimates of gene size similar to that of large organic molecules. Genes have the power of self-propagation. Sometimes they manifest themselves by a change in reaction velocity as in Dunn and Landauer's creeper fowls. Here the different parts of the embryo are affected in order of their relative growth rates.

There is no critical evidence for the inheritance of effects of alcohol. With cancer there is limited evidence. There are benign and malignant hereditary tumors in Drosophila, pigment sarcomas in the horse, and Xeroderma pigmentum in man. The human polyposis adenomatosa favors cancer development in the large intestine. Other hereditary tumor types are glioma retinæ, cartilaginous exostoses, multiple fibro-neuromatoses. Adeno-carcinoma uteri, fibroadenoma of the left breast, cancer of the larynx, and sarcoma of the right testis have been found in identical twins. Inheritance of rodent tumors is shown by Strong, Lynch and Slye, while Krebergs finds that the time of onset of tumor formation may differ for different strains. Loeb and Lathrop have evidence that suggests ovarian activity as necessary to mammary tumor formation in mice. The hereditary mechanism of tumor susceptibility has not been determined with any degree of accuracy.

Applied Human Genetics

Chapter V takes up human applications. It shows that by inbreeding we may recapture valuable recessives, but may also bring to the surface undesirable recessives. Where race-crossing has been decried one may look for "race-degeneration motives." In a civilized humanity where cross-breeding prevails, pure races no longer exist.

We can cut off dominant pathological traits; we are quite limited in attempting to eliminate recessives and sex-linked traits. "There is, moreover, every reason to object to the uncritical enthusiasts who in all countries mislead the public by giving a wrong impression of the effectiveness of the sterilization measures recommended," whereas those who are affected by really serious abnormalities do not propagate their numbers. We know what we want to breed for in animals; we have no human goals, and many types are need-

ed in a highly organized society. The cry that lowered birth rate in "good families" will result in race suicide, is fallacious, because good and bad are probably distributed pretty much at random among the social strata.

Physicians, by consulting genetic texts, may pass out much good advice, but their "judgment should always be given with the reservation involved in the fact that genetics primarily deal with probabilities." "All the valuable acquirements which conscientious parents may accumulate in the course of a lifetime are genetically a dead investment" but may be of considerable importance environmentally in the developing of their offspring.

Splendid orthodox line cuts serve as textfigures. The half-tones crowded together following the text constitute a veritable chamber of horrors. Too bad that Mendel and his cloister brethren must forever dwell on the same page with examples of degenerate toe nails, brachydactyly, and woolly hair! Ophthalmologists may smile at "bull eyes" instead of "ox-eyes." Mammalogists will gasp at "tumors of the breast in mice." When ordering your copy, consult the back of the jacket, where it is listed at $2.75, instead of the front flap, where it is priced at $3.50.*

CLYDE E. KEELER
Howe Laboratory and Bussey Institution

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THE FUTURE OF THE WHITE RACE

DR. Burgdörfer's little volume† is one of the many recent German publications which voice a widespread alarm over the declining birth rate of the white race, and especially the peoples of Nordic stock. As the author points out, the birth rate of most countries of northern, western, and central Europe has fallen to such an extent that, were it not for their favorable age composition, their inhabitants would be actually decreasing in numbers. The birth rate of other European countries has also been declining, and apparently it will be only a few years before they will be in the same situation as Germany, France, and England. The United States, Canada, Australia, New Zealand, and the white population of South Africa are attacked with the same fatal malady which now has Europe in its grip.

During the last few centuries the white race increased with extraordinary rapidity and spread over extensive areas of the earth, but now, like a plant which has exhausted its energies in the period of vigorous growth, it has come to show signs of failing vitality. It is affected by the same kind of internal disorders which led to the decline of the Assyrians, Egyptians, Greeks, and Romans. In the near future the whites in South America, South Africa, and Asia will be pressed to the wall by the increasing numbers of the colored races. Thinly settled Australia must sooner or later succumb to the population pressure of the teeming millions of Asia; and the white population of the United States is destined to become increasingly dark in color owing to the preponderant fertility of its Negro population. The Negroes in the United States have not only increased in numbers, but their rate of increase has become greater than it was during the previous decade, while that of the whites has gone continuously downwards. According to Burgdörfer it is only through immigration from Europe that the white inhabitants of the United States will be able to hold their own with the Negroes in the struggle for numerical supremacy.

Is the white race inevitably destined to have its day and cease to be? Dr.

* It won't do any good, because the publisher informs us that the price on the back cover is a mistake, and he invokes the principle of "first come, first served" to maintain the front flap price.—EDITOR.

† BURGDÖRFER, F., *Sterben die Weissen Völker?* Pages, 89. (Munich, Callwey), 1934.

Burgdörfer thinks not. We can save ourselves from the yellow peril, the black peril, and the perils of other colors which loom up in various horizons if we have the determination and the foresight to take the proper steps to avoid the catastrophe. Here is where the great German people who are now almost in the van in the race toward extinction can perform a great service to humanity, not only in rescuing themselves from becoming a dwindling and feeble folk, but in pointing the way in which other peoples of the white race can solve the same problem.

This volume is written in a very serious spirit. Despite the present sombre outlook for the white race the author is still confident that Germany will be able to solve her population problems and become the torch bearer for the rest of white humanity. Dr. Burgdörfer seems to be encouraged over the results already achieved in the program of race rejuvenation undertaken by the Hitler regime. People are marrying more than a while back! Up to August, 1933, there were over 7 per cent more children born than in the corresponding months of the previous year! Unemployment is being reduced, and the defectives are being sterilized! Nevertheless, these "erfreulich" results do not justify a passive and tranquil attitude. They should serve rather as a stimulus to further effort. A reformer, of course, must not lose courage. But does the author seriously believe that the measures he describes will rejuvenate the German people? To some readers he will probably appear like a drowning man hopefully catching at straws. To others he will seem to be needlessly alarmed. But whatever may be thought of the author's fears and hopes, he has presented a very important problem in a clear and readable manner.

S. J. Holmes
University of California

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A SCIENTIST IN THE EARLY REPUBLIC

THE settling and civilizing of the American Continent was such a colorful performance that the attention of our historians has been somewhat limited to those Colonists who participated directly in the task, that is, to our outstanding soldiers and statesmen. We are just beginning to realize that the Americans of two hundred years ago were an exceptionally versatile lot, and that their scientific achievements are far too important to be ignored. The accomplishments of such exceptional individuals as Benjamin Franklin and Thomas Jefferson are of course well known but the fact that other leading statesmen contributed to our scientific development has never received the attention it deserves. It is only necessary to describe the scientific work of a Governor of Connecticut (John Winthrop), a Lieutenant-Governor of New York (Cadwallader Colden) and a Governor of Pennsylvania (James Logan) to show that the political leaders of the Colonies were somewhat different from their modern homologues. A surprisingly large number of the Colonists were Fellows of the Royal Society.

This scientific activity continued well into the period of the Early Republic and while no one American scientist deserves to be ranked with the great European leaders of the early nineteenth century, several of them were important enough to secure world-wide recognition. Perhaps none of these carried on the tradition of American versatility as well as did Samuel Latham Mitchill whose story is told by Courtney Robert Hall.*

Mitchill was born at North Hempstead, Long Island, in 1764. He studied at the University of Edinburgh and returned to New York in 1787 with

*Hall, Courtney Robert, *A Scientist in the Early Republic, Samuel Latham Mitchill (1764-1831)*. Columbia Univ. Press, New York, 1934.

the degree of Doctor of Medicine. Almost at once he became the leading physician in the city and his tremendous and never failing curiosity and energy caused him to participate in most of the activities of the new and growing town. In 1788 he was appointed one of the commission to negotiate with the Indians in Western New York for the purchase of lands and in 1791 he became a member of the New York State Legislature. In 1792 he was appointed Professor of Natural History at Columbia College and from 1793-95 Professor of Botany. In 1801 he resigned his chair at Columbia to accept a seat in Congress. He was a member of the House of Representatives until 1804, a Senator until 1809 and again a Representative until 1813. In 1807 he became Professor of Chemistry at the College of Physicians and Surgeons in New York, in 1808 he became Professor of Natural History and in 1820 Professor of Botany and Materia Medica. In 1826 he resigned in order to help found the Rutgers Medical College of which he became Vice-President. He helped to found the New York Literary and Philosophical Society and the Lyceum of Natural History. He was surgeon general of the state militia in 1818. He died in 1831.

This brief list of Mitchill's occupations does not give an adequate picture of his manifold activities. He assisted Robert Fulton in securing state aid for his steam boat; during the war of 1812 he served on a commission to supervise the construction of steam war vessels; he attempted to reform chemical terminology and entered into the phlogiston controversy with Priestley; he founded the *Medical Repository* in 1797 and contributed to it many scientific articles; he made numerous geological and botanical explorations; he was the new-world authority on fishes; he built up a private museum; he tried to have the name of the United States changed to "Freedonia"; he even invented a medical panacea, i. e., disease was caused primarily by the accumulations of organic acids ("Septon") in the body and health could be secured by taking alkalies. This fanciful theory brings to mind very forcibly some of the modern radio ballyhoo.

Obviously the life and work of such a man as Mitchill should be recorded and evaluated. Hall's study is completely adequate. He concerns himself not only with Mitchill as an individual but with the period in which he lived. His account of the status of the several sciences in the America of the early nineteenth century is an important contribution to our knowledge of our own scientific background.

CONWAY ZIRKLE
University of Pennsylvania

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Books Received

***BOOKS** are acknowledged in this column as received, and such acknowledgment must be regarded as sufficient return for the courtesy of the sender. As far as space permits, books that contain material of special interest to the readers of the* JOURNAL *will be reviewed in later numbers.*

CONSTRUCTIVE EUGENICS AND RATIONAL MARRIAGE, *by* MORRIS SIEGEL, M. D. Pages, 196. McClelland & Stewart, Limited, Toronto, 1934.

GENETICS OF ZEA MAYS, *by* WILLIAM H. EYSTER. Pages, 392, 91 illustrations. Reprint from *Bibliographia Genetica*. Martinus Nijhoff, The Hague, 1934.

BLOOD GROUPS AND BLOOD TRANSFUSION, *by* ALEXANDER S. WEINER. Pages, 220, 41 illustrations. Price, $4.00. Charles C. Thomas, Springfield, 1935.

THE SCIENTIFIC BASIS OF EVOLUTION, *by* THOMAS HUNT MORGAN. Second Edition. Pages, 306, 45 illustrations. W. W. Norton & Company, New York, 1935.

GRUNDRISS DER CYTOLOGIE, *by* LOTHAR GEITLER. Pages, 295, 209 illustrations. Price, 19.20 RM. Gebrüder Borntraeger, Berlin, 1935.

THE CHALLENGE TO LIBERTY, *by* HERBERT HOOVER. Pages, 212. Price, $1.75. Charles Scribner's Sons, New York, 1935.

THE PRINCIPLES OF HEREDITY, *by* LAURENCE H. SNYDER. Pages, 385, 153 illustrations, index. Price, $3.00. D. C. Heath and Company, Boston, 1935.

A new assay at informing and interesting beginners in genetics in genes and their consequences. Excellently illustrated, and first glance indicates, thoroughly up to the minute. Try to find a discussion of salivary chromosomes in any other textbook! The Datura chromosomal mutations, X-ray genetics and gene frequency methods of attacking problems of human inheritance are recent developments treated at length.

BIOLOGY FOR EVERYMAN, *by* J. ARTHUR THOMSON. Volumes I and II. Pages, 1559, 500 illustrations. Price, $5.00. E. P. Dutton & Co., Inc., New York, 1935.

GUIDING YOUR CHILD THROUGH THE FORMATIVE YEARS, *by* WINIFRED DE KOK. Pages, 191. Price, $2.00. Emerson Books, Inc., New York, 1935.

SEX PRACTICE IN MARRIAGE, *by* C. B. S. EVANS. Pages, 128. Price, $1.95. Emerson Books, New York, Second Edition, 1935.

THE GENETICS OF GARDEN PLANTS, *by* M. B. CRANE and W. J. C. LAWRENCE, John Innes Horticultural Institution. Pages, 263, 53 illustrations, and 42 tables. Price, 10/6. Macmillan and Co., London, 1934.

Bacon tells us that "God Almighty first planted a garden," and in a garden at Brunn, Mendel found the key to heredity. Both (or even all three) would perhaps be stumped by "aneuploid," "amplidiploid," and "hemyzygosity," terms which no progressive gardener should be without in 1935.

PSYCHO-ANALYSIS FOR TEACHERS AND PARENTS, *by* ANNA FREUD. Translated by Barbara Low. Pages, 117. Price, $1.75. Emerson Books, Inc., New York, 1935.

And a few Books on Ecology—Human and Otherwise

THE UNIVERSE AND LIFE, *by* H. S. JENNINGS. Pages, 95. Yale University Press, New Haven, 1934.

How cosmic ecology looks to a biologist.

THE STRUGGLE FOR EXISTENCE, *by* G. F. GAUSE. Pages, 163. The Williams and Wilkins Company, Baltimore, 1934.

Paramecium meets Didinium under the microscope and the experimental study of the survival of the fittest is under way!

TREND ANALYSIS OF STATISTICS, *by* MAX SASULY. Pages, 421. The Brookings Institution, Washington, 1934.

Higher mathematics for human ecologists.

INTERNAL MIGRATION IN THE UNITED STATES, *by* C. WARREN THORNTHWAITE. Pages, 52, maps, graphs. Price, $1.00. Study of Population Redistribution. University of Pennsylvania Press, 1934.

MENTAL HEALTH, Past, Present, and Future, *by* ARTHUR HILER RUGGLES. The Colver Lectures, 1932. Pages, 104. Williams and Wilkins, Baltimore, 1934.

THE PATIENT AND THE WEATHER, Volume II, Autonomic Dysintegration, *by* WILLIAM F. PETERSEN with the assistance of MARGARET E. MILLIKEN. Pages, 530, 249 illustrations. Price, $6.50. Edwards Brothers, Inc., Ann Arbor, 1935.

More ado about the ecology of the subconscious, and other matters.

HABITAT, ECONOMY, AND SOCIETY, *by* DARYLL FORDE, Professor of Geography and Anthropology in the University of Wales. Pages, 500, maps, and 109 illustrations. Price, 15/. Methuen Co., Ltd., London, 1934.

Another kind of human ecology.

A HISTORY OF EMBRYOLOGY, *by* JOSEPH NEEDHAM. Pages, 274, 16 illustrations. Price, $4.00. Cambridge University Press, 1934.

A summary of what we have in the way of quaint beliefs and exact knowledge of prenatal ecology, from early Egypt to modern times.

ALASKA NATIVES, A Survey of Their Sociological and Educational Status, *by* H. DEWEY ANDERSON and WALTER CROSBY EELLS. Pages, 472, 97 illustrations, index. Price, $5.00. Stanford University Press, 1935.

THE EUGENICS EXHIBIT AT CHICAGO

A Description of the Wall-Panel Survey of Eugenics Exhibited in the Hall of Science, Century of Progress Exposition, Chicago, 1933-34.

HARRY H. LAUGHLIN
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THE Century of Progress Exposition was the first world's fair to include eugenics as a matter of course in the classification of the basic sciences. For this reason the exhibit has an historic interest, rather greater than its size, and an account of it is consequently of value as a reference record. The exhibit was not highly technical. It was designed primarily to be understood by the average intelligent and interested visitor. This was specification number one.

In the preparation of this exhibit it was necessary to make haste, to work without special funds, and to fit the exhibit to a wall space six feet wide and forty feet long. This was specification number two.

This stretch of wall constituted the space officially alloted in the Hall of Science to the subject of eugenics. The position of eugenics in the next world's fair will depend basically upon the development of eugenics in the meantime; the classification and space-allotment committees will reflect the actual status at that time.

An accurate general survey of the whole science of eugenics was desired by the exposition management, but because of the limitations of time, space, and money, it was deemed fitting to build the exhibit around some special subject in the general field, and to trace such special theme through a number of ramifications and contacts. An exhibit of this sort would enable the visitor, if interested, to find out what eugenics is all about. This was specification number three.

What special subject then would best fulfill these specifications? If we attempted to list the several major factors which constitute the main body of eugenics as a science, we should name the following purposes of study:

(1) To find the rules which govern the inheritance of specific human qualities—physical, mental, and spiritual.

(2) To analyze and weigh the factors which govern mate-selection in reference to hereditary quality.

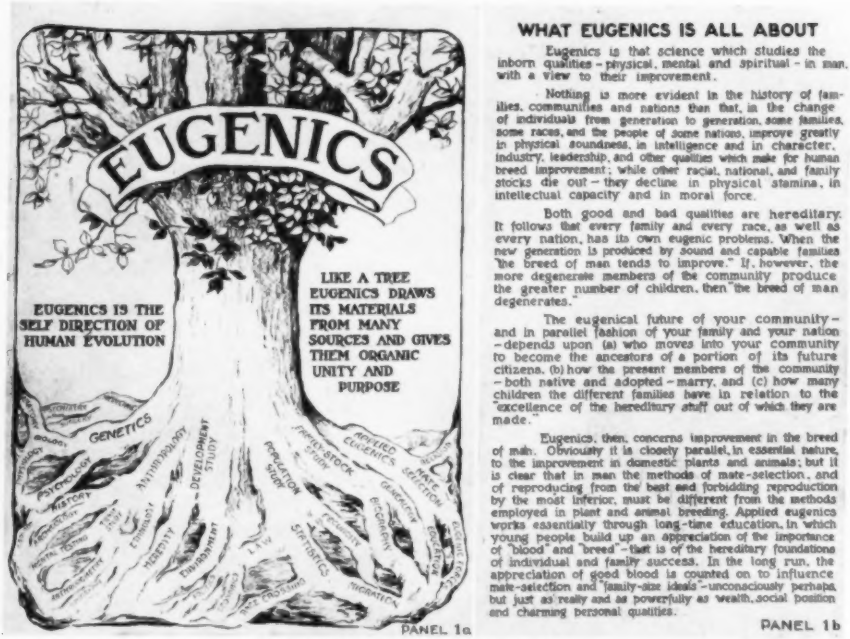
(3) To determine the forces which govern differential fertility — that is, which families have many children and which few, in reference to hereditary quality.

(4) To determine which portions of the population will survive to and through the reproductive period and on to the end of social usefulness, and which will lack survival strength—all in reference to inborn quality.

(5) To study the history and forces of human migration to determine which individuals, in reference to racial and hereditary quality as potential breeding-stock, move from one geographic region to another.

It was decided finally to try to meet the specifications above listed by building the exhibit around the general subject: "Pedigree-study in Man." The claim that man, unlike the plants and animals, is not subject to the laws of biological inheritance, particularly in his finer intellectual and moral qualities, is the last stand of the "anti-herediterians." Eugenics, like all science, must find and study the facts and report the evidence for critical interpretation—whether such facts and conclusions be pleasant or unpleasant.

So it worked out that the exhibit consisted of four large wall panels or charts. It was necessary in their design to attempt to present, by subject and method, sound material which would attract the attention of the aver-


EUGENICS
EUGENICS IS THE SELF DIRECTION OF HUMAN EVOLUTION
LIKE A TREE EUGENICS DRAWS ITS MATERIALS FROM MANY SOURCES AND GIVES THEM ORGANIC UNITY AND PURPOSE
GENETICS
PSYCHOLOGY
ANTHROPOLOGY
DEVELOPMENT STUDY
PANEL 1a
WHAT EUGENICS IS ALL ABOUT
Eugenics is that science which studies the inborn qualities – physical, mental and spiritual – in man, with a view to their improvement.
Nothing is more evident in the history of families, communities and nations than that, in the change of individuals from generation to generation, some families, some races, and the people of some nations, improve greatly in physical soundness, in intelligence and in character, industry, leadership, and other qualities which make for human breed improvement; while other racial, national, and family stocks die out – they decline in physical stamina, in intellectual capacity and in moral force.
Both good and bad qualities are hereditary. It follows that every family and every race, as well as every nation, has its own eugenic problems. When the new generation is produced by sound and capable families "the breed of man tends to improve." If, however, the more degenerate members of the community produce the greater number of children, then "the breed of man degenerates."
The eugenical future of your community – and in parallel fashion of your family and your nation – depends upon (a) who moves into your community to become the ancestors of a portion of its future citizens, (b) how the present members of the community – both native and adopted – marry, and (c) how many children the different families have in relation to the "excellence of the hereditary stuff out of which they are made."
Eugenics, then, concerns improvement in the breed of man. Obviously it is closely parallel, in essential nature, to the improvement in domestic plants and animals; but it is clear that in man the methods of mate-selection, and of reproducing from the best and forbidding reproduction by the most inferior, must be different from the methods employed in plant and animal breeding. Applied eugenics works essentially through long-time education, in which young people build up an appreciation of the importance of "blood" and "breed" – that is of the hereditary foundations of individual and family success. In the long run, the appreciation of good blood is counted on to influence mate-selection and "family-size ideals" – unconsciously perhaps, but just as really and as powerfully as wealth, social position and charming personal qualities.
PANEL 1b

THE INTRODUCTORY PANEL
Figure 11

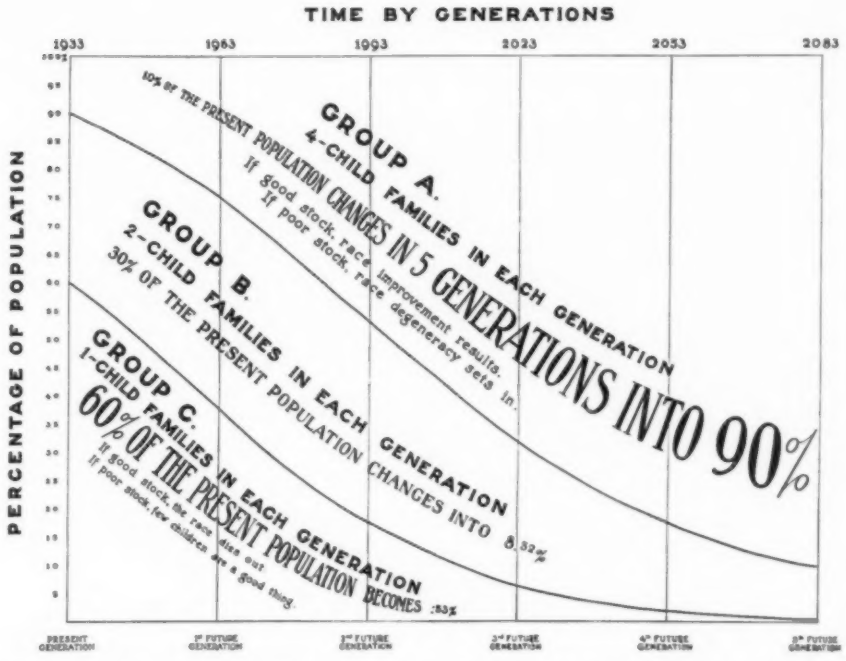
The eugenics exhibit at the Century of Progress Exposition consisted of a series of four wall panels showing the aims of eugenics as exemplified in human pedigree studies. The first panel was a graphic representation of the relation of eugenics to other sciences and a brief introductory statement.

age intelligent world's fair visitor, and would also enable him to get the basic idea of what eugenics is all about,—how it works, with what specific subjects it deals, and in what ways it could serve the individual, his family, his community and his race. The visitor who showed special interest in the subject would desire also to criticize the facts assembled and the principles deduced by eugenics, to compare them with his own first-hand knowledge and experience, and to learn in what direction this new science is moving.

When installed, the four-chart eugenics exhibit was favorably placed along a well-lighted wall in one of the main wide corridors of the Hall of Science, near other biological and particularly anthropological and genetic subjects. In front of the series of panels, which were placed in logical order from left to right, there was built a guard-rail about waist high and four feet from the exhibit. Thus, so far as physical set-up was concerned, visitors found it quite convenient to start with chart one at the beginning and to pass down the line, "glancing at, inspecting or studying" the charts in logical sequence.

The panels ran as follows:

PANEL 1A. "The Eugenics Tree." This symbolic treatment defines eugenics as "the self-direction of human evolution," and it extends the metaphor by stating that "like a tree eugenics draws its materials from many sources and gives them organic unity and purpose." It is half diagnostic and half descrip-


HOW FAMILIES, COMMUNITIES, RACES AND NATIONS MAY CHANGE GREATLY IN CAPACITY WITHIN A FEW GENERATIONS.
TIME BY GENERATIONS
1933
1963
1993
2023
2053
2083
PERCENTAGE OF POPULATION
GROUP A.
4-CHILD FAMILIES IN EACH GENERATION
10% OF THE PRESENT POPULATION CHANGES IN 5 GENERATIONS INTO 90%
If good stock, race improvement results.
If poor stock, race degeneracy sets in.
GROUP B.
2-CHILD FAMILIES IN EACH GENERATION
30% OF THE PRESENT POPULATION CHANGES INTO 8.32%
GROUP C.
1-CHILD FAMILIES IN EACH GENERATION
60% OF THE PRESENT POPULATION BECOMES .33%
If good stock, the race dies out.
If poor stock, few children are a good thing.
PRESENT GENERATION
1st FUTURE GENERATION
2nd FUTURE GENERATION
3rd FUTURE GENERATION
4th FUTURE GENERATION
5th FUTURE GENERATION
THIS SORT OF THING IS GOING ON ALL THE WHILE. IT IS THE MAIN FACT UPON WHICH INDIVIDUAL FORTUNES AND NATIONAL HISTORY ARE BASED.

EFFECT OF DIFFERENTIAL BIRTH RATES ON FUTURE GENERATIONS

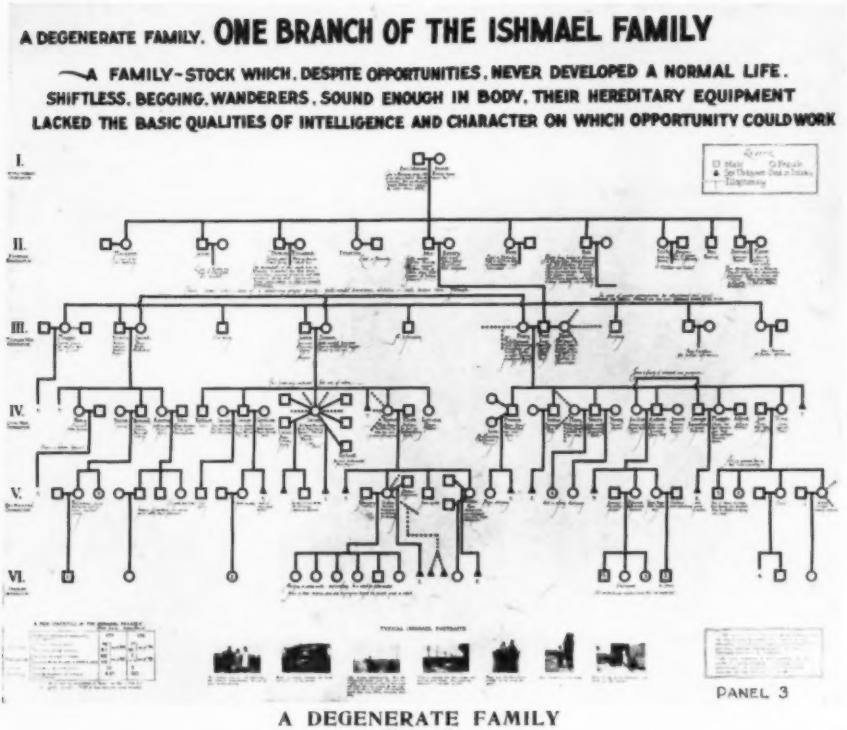
Figure 12

The second panel of the series showed the "turn over" in population produced by differences in birth rates. It is easily seen from this chart that a group which adopts the one-child family ideal will, five generations hence, have a very small representation in the population, as compared with a group having an average of four children per family. This chart presents in summary form one of the major problems of eugenics: to encourage the better endowed part of the population to avoid a suicidal reduction in birth rate.

tive. It is "the picture of the introductory chapter of the principles of eugenics."

PANEL 1B, in the same section, consists of a descriptive statement entitled: "What Eugenics is all about." This tells its own story.

PANEL 2 is a chart entitled: "How Families, Communities, Races and Nations May Change Greatly in Capacity Within a Few Generations." The main point of this chart is to show that, no matter how strong in quality or numbers a particular nation or family might have been a few generations ago, nor how correspondingly weak another family or race might have been, a census now—and a few generations later—


A DEGENERATE FAMILY. ONE BRANCH OF THE ISHMAEL FAMILY
A FAMILY-STOCK WHICH, DESPITE OPPORTUNITIES, NEVER DEVELOPED A NORMAL LIFE.
SHIFTLESS, BEGGING, WANDERERS, SOUND ENOUGH IN BODY, THEIR HEREDITARY EQUIPMENT
LACKED THE BASIC QUALITIES OF INTELLIGENCE AND CHARACTER ON WHICH OPPORTUNITY COULD WORK
I.
II.
III.
IV.
V.
VI.
PANEL 3

A DEGENERATE FAMILY
Figure 13

Pedigree chart of the Ishmael family giving a six generation summary history of this group. The details regarding the members of the family were lettered in on the chart and were readily legible in the large wall panel. In so small a reproduction they cannot be read for it was not possible to reproduce in halftone the lettering in legible form when so greatly reduced. These two panels showing the Ishmael and the Roosevelt pedigrees were placed side by side on the exhibit wall in order to invite the visitor's attention to both the negative and the positive aspects of eugenics.

Generally a group of five or six visitors was found in front of these panels, some trying to find out what eugenics is all about, others trying to figure out what differential fertility means, and possibly others tracing some valuable or some degenerate quality through successive generations in the same family. It was interesting to mingle with these visitors, to join in conversation with them, and through their comments to seek their understanding and criticism of eugenics in general, or in particular of some fact or principle shown in the exhibit.

It may be safely said that the average American with "upper grammar school plus" intelligence understands quite definitely what sound hereditary stuff—physical, mental, and spiritual—means. The concept is gaining adherents and bids fair to become a generally accepted commonplace in another generation. Such an appreciation would, with little doubt, be reflected in the inborn quality of future generations of the American people.

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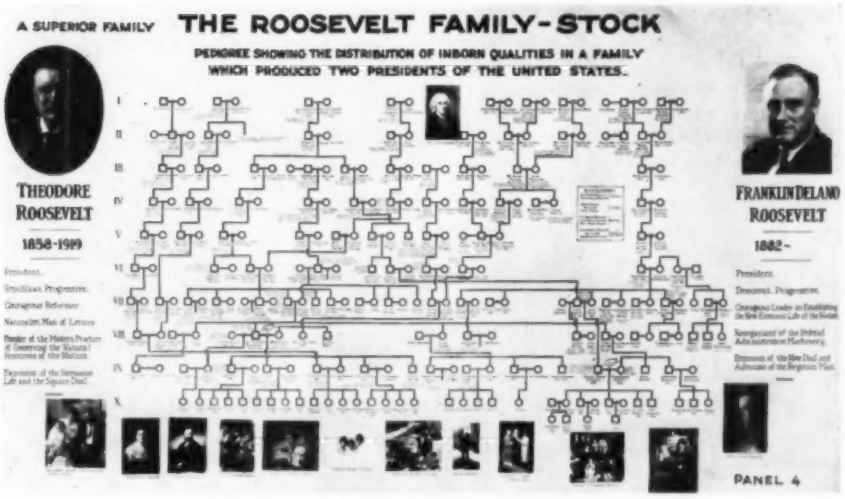
generally shows great change in both absolute and relative numbers, and in inborn quality, to have gone on with the turnover of population through successive generations. Such changes depend upon the major factors of (a) migration, (b) how the members of the particular groups marry, (c) how many children are produced per marriage, and (d) how many of these children survive through the period of reproduction and social usefulness. Each of


A SUPERIOR FAMILY
THE ROOSEVELT FAMILY-STOCK
PEDIGREE SHOWING THE DISTRIBUTION OF INBORN QUALITIES IN A FAMILY WHICH PRODUCED TWO PRESIDENTS OF THE UNITED STATES.
THEODORE ROOSEVELT
1858-1919
FRANKLIN DELANO ROOSEVELT
1882-
PANEL 4

A FAMILY PRODUCING TWO PRESIDENTS

Figure 14

Three family groups have contributed two presidents to the United States. The Roosevelts trace back to Jonathan Edwards (portrait in center) and Elizabeth Tuthill, a Puritan couple many of whose descendants have contributed to the progress of the United States. The two presidents who have sprung from this line are indicated in the pedigree chart by the pointing hands.

these four elements, *a*, *b*, *c*, and *d*, is by eugenics treated from the standpoint of a difference in inborn or hereditary stuff—physical, mental and spiritual. This chart presents time by generations moving from left to right across the panel; while the vertical spaces show division of the population by inborn quality and ancestral descent.

The average intelligent American who visited the World's Fair may not have had advanced mathematical or statistical training in handling graphs, but such an American is a good "puzzle worker." Thus, when interested, the usual visitor had little difficulty in reading the meaning of Chart Number 2 on "The Outcome of Differential Fertility." It was necessary only that he apply himself for a few minutes to find out how the thing worked.

PANEL 3 is entitled "The Ishmael Family" and shows one branch of the old, extensive and degenerate Ishmael tribe which was studied intensively, by the Eugenics Record Office in Indiana, a number of years ago.

PANEL 4 shows a superior family, "The Roosevelts." These two charts were placed side by side for the purpose of contrasting qualities in the hereditary equipment of different family-stocks. Perhaps the Roosevelt chart attracted more attention than the Ishmaels. Visitors studied the Ishmaels with interest, but the average person was apt after a little while to brush the Ishmael chart aside—apparently with the judgment "human culls"—rather than to engage in further analytical study. The Roosevelt family however, was a constructive pedigree showing the distribution of inborn qualities in a family-stock which produced two presidents of the United States.

Presidential Pedigrees

Comparative historic comment on Chart Number 4 ran as follows: Besides the Roosevelts, two other families,

the Adams and the Harrison, each produced two presidents. Here again the matter of hereditary stuff interacting with environment and opportunity comes into play. It is interesting to note how a democracy which elects its own presidents, and is so jealous of monarchy and of the inalienable right of the citizen, and with so many honest and capable leaders striving for the presidency, should elect among its presidents, two Adamses, father and son, and seriously consider a third—a grandson; two Harrisons, grandfather and grandson; and two Roosevelts, distant cousins, with Anna Eleanor Roosevelt, the wife of Franklin D. Roosevelt, also born of Roosevelt stock. Thus in choosing the head of the state, America, without prejudice, three times returned to the family-stock of a previous president. In this the republican form of government again shows its superiority and flexibility. If the nation wants two members from the same family-stock, it selects them. If, however, it finds a better leader in a new or different stock, it is free to make the selection. Monarchy is handicapped by forcing leaders on the nation without so much regard for the selective factor.

In the Exhibit of the Third International Congress of Eugenics in New York in 1932, pedigrees of three presidents were shown in considerable detail: Washington, Lincoln, Roosevelt. Washington was known to be an aristocrat. Pedigree analysis amply upheld the claim. Lincoln, on the other hand, was held to be a commoner, and the average man would doubtless say it was useless to study the Lincoln pedigree. But when the Lincoln antecedents and near-kin were studied critically, these backwoodsmen were found to be rising to civic and industrial leadership in their respective pioneer communities. They were blacksmiths and mechanics and justices of the peace—the highest positions in the backwoods country. It required superior inborn stuff to make a good village blacksmith four generations ago in Kentucky. Biologically the inborn pioneer qualities of Lincoln's near-kin were potential aristocrats *sans reproche*.

The average visitor guided himself about the World's Fair by means of maps, guide books and by "asking a policeman." The professional guide for a fee had generally to find entertainment or amazement, but he was not often used. When the hunted exhibit was found, or an interesting display stumbled upon, the visitor often found persons in charge to explain the particular display, but in many other cases it was left to the visitor to make his own inspection and interpretations. Because no one was stationed permanently at the eugenics exhibit it was all the more necessary that the charts be self-explanatory and well adapted for conversation among mutually interested visitors. The eugenics exhibit was like most such displays at the World's Fair in that a small group of half a dozen or so strangers was usually assembled at the exhibit trying to find out what it was all about or how it worked.

Because the members of such groups were mutually interested they struck up conversation and discussion with little difficulty. Among such groups at the eugenics display it was as a rule not difficult to find at least one person — high school boy, farmer, school teacher, parent, doctor, lawyer, merchant—lingering before the exhibit, and who with little urging would explain to the newly assembled group how populations change in inborn quality, or how the pedigree principle is just as applicable to human families as to domestic plants and animals, or who would elucidate some other principle in eugenics, and would point out the specific evidence on the charts, or would add his own experience for or against.

The average visitor glanced at the Eugenics Tree, paused a little before the panel on "What Eugenics is all about," and then had his attention arrested for a while by the "Roosevelt pedigree-chart." Then he moved on. However, many who were especially interested moved back to Panel 1 and worked

through the exhibit more or less systematically.

The Pedigree-Idea

Human family-stocks and strains of plants and animals in their hereditary behavior present basic analogies too close to dispute successfully. While this analogy was not brought out directly by the exhibit, the facts were presented in such a manner that the visitor with a little knowledge of plant and animal breeding readily supplied the analogy himself. In this the intelligent farmer who treasured hereditary quality in his plant and animal stocks had the necessary background for building up in his own mind the basic pedigree concept of eugenics. The parallel with his own efforts to improve a breed of poultry, hogs or cattle on his own farm was too close to be denied mental reflection when human pedigrees were brought to his attention.

Thus the pedigree-idea spread,—that is, the general appreciation of hereditary quality. Historically it developed first in reference to cattle and horses, then spread to other farm animals, then to grains and other plants, and last of all to man. Within the human realm, as a principle of general appreciation, it applied first to racial traits. Chinese produced Chinese; Negroes, Negroes; and white people, white people—if the "blood," that is the pedigree, was clear. Later the factor of heredity was studied and appreciated in human anatomical traits, then in physiological qualities, then in intelligence and specialized mental capacities, and now the last group of human qualities—those of the character and personality are being analyzed, diagnosed, weighed, measured and traced in human families to find the rules of inheritance of the several basic elements of personality. This latter work is one of the major joint tasks of psychology and eugenics for the next decade of research.

In any good eugenics exhibit there must always be a section for "Heredity and Environment." Such an exhibit must bring out clearly how both heredity and environment are important,—each a vital factor in the development of the individual,—not especially which is *more* important as a whole, but in the particular case what part each plays in development. When it comes to passing these basic qualities on to the next generation, it is the ancestral stock which counts; it is heredity rather than environment which is passed on. Thus in the pedigrees shown in Panels 3 and 4 the factors of environment must be taken into consideration and either equalized, or, if different, duly weighed in the analysis. Difference in the lives and conducts of individuals are accounted for only by the proper appreciation of the relative values of heredity and environment, that is, a determination of the reaction between the basic inborn qualities of body, mind and spirit, with the physical, social, economic, educational and spiritual surroundings.

The Next Exhibit

There were, of course, many other phases of eugenics which could have been shown to advantage; for example, the entire exhibit of the Third International Congress of Eugenics which was held in New York City in the American Museum of Natural History in 1932, and which filled the whole exhibit hall with some thirty booths, and ten thousand square feet of wall space, might well have been shown at the Century of Progress Exposition.*

When the next World's Fair is held, it would seem fitting for eugenical organizations the world over to present to the Director General of Exhibits of such a fair, a photographic and documentary history of the exhibits held at the three International Congresses of Eugenics—in London in 1912, in New York in 1921, and the third in New

*See EUGENICAL NEWS for November-December, 1932. See also "A Decade of Progress in Eugenics, A Report of the Third International Congress and Exhibit of Eugenics," Harry H. Laughlin, editor, Part Two of which book is a description of the exhibits.

York in 1932—as a gauge for the possibilities of eugenics as the subject for a satisfactory exhibit in science.

The Century of Progress Exposition, intended to be a universal world's fair, admitted for the first time in such a fair a section on eugenics. As the science of eugenics makes good, and develops more soundly and definitely, the next World's Fair will show even more completely than was shown at the specialized Exhibit at the Third Eugenics Congress in New York in 1932, the nature of eugenics as a pure science, and also its use in the interpretation of history, and in the application to breed-improvement in man —a practical science which can be used by the individual, the family, the community, the state, nation, and the race.

TWO RELATED HAIRLESS MUTATIONS IN THE NORWAY RAT

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HAIRLESSNESS or hypotrichosis has appeared recently as an hereditary character in a number of different species of mammals. Thus far two distinct and independent occurrences of a mutation of this type have been reported in the Norway Rat *Rattus norvegicus*, Roberts,[1,2] presented data upon one; Wilder, et al[3] described a second. The published descriptions and data indicated a high degree of similarity if not identity. Each proved to be recessive to the normal condition. Preliminary tests showed no evidence of a genetic linkage of either hairless gene with the color gene.

Through the kindness of Doctors Roberts, Bethke and Spencer the writer had at the Laboratory of Vertebrate Genetics, University of Michigan, a small stock of each of these hairless mutations during 1933. A careful comparison of specimens of the two stocks revealed no significant differences of appearance in the hairless character although the rats were obviously different in other physiological and structural characters. A difference in the location and arrangement of the skin folds in rather aged animals distinguished the hairless rats of the two strains. Breeding tests were necessary to determine whether these two mutations were due to different genes and perhaps located in different chromosomes or whether they involved only one gene and were therefore allelomorphs. The following series of matings was devised to discover the genetic relationship:

1. Wooster hairless *hh* ♂ × Roberts hairless *hh* ♀ produced 17 young. All were hairless *hh*.
2. Roberts hairless *hh* ♂ × Wooster heterozygous *Hh* ♀ produced 43 young. They were 12 Normal *Hh* ♀♀; 11 Normal *Hh* ♂♂; 11 hairless *hh* ♀♀; 9 hairless *hh* ♂♂.
3. Hairless animals from each of these crosses mated *inter se* produced 102 young all of which were hairless, *hh*.

These results indicate rather definitely that these two hairless mutations are either identical or very similar allelomorphs.

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3. WILDER, WILLARD, R. M. BETHKE, C. H. KICK and W. P. SPENCER, 1932. A Hairless mutation in the rat. *Journal of Heredity*, 23:481-484.

LOCATING GENES ON SALIVARY CHROMOSOMES

Cyto-Genetic Methods Demonstrated in Determining Position of Genes on the *X* Chromosome of *Drosophila melanogaster*

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University of Texas

IN a recent article in this journal Painter[7] gave an account of how salivary gland chromosomes came to be studied at this laboratory, and briefly discussed some of the major problems which this new method has allowed us to attack. Foremost among these is the question of the morphological position of the genes along the chromosomes. As he has pointed out, there are several different ways in which this can be determined. We can study breaks (accompanied by translocations) which have occurred between two known gene loci, and having found where the chromosome is actually broken we can say that genes *a* and *b*, for example, lie to the right and left of a given morphological point. This is the method which Painter has used in making new cytological maps of the *X*[4], the second[6], and third[5] chromosomes, largely because this was the main type of aberration available. It was recognized at the very beginning of the work that simple translocations would only occasionally allow us to localize genes to very small areas along the chromosomes. At the same time that translocations are produced by irradiation, however, Dr. J. T. Patterson[8] has shown that very often small sections are deleted from a single chromosome and this seemed to offer a more exact and a much simpler method of determining the position of gene loci. Knowing what genes are absent and what part of the chromosome is missing, we can say that these gene loci lie within the deleted section. It was therefore suggested to the writer that he use this method and apply it to the location of gene loci along the *X* chromosome. A preliminary statement of the problem, the methods employed, and some of the results obtained has already been published (Mackensen[1]).

In the present article it is proposed to present the evidence which has made it possible to localize eight genes along the *X* chromosome to very small areas, in two instances to one "band" or a part of a band. At this point the author wishes to express his appreciation for the assistance given him by Dr. T. S. Painter from the cytological side, and Dr. J. T. Patterson and Mr. Wilson Stone from the genetic standpoint.

Material and Methods

We had at this laboratory among our stocks a few deletions obtained by Patterson[8], but most of the cases described below were obtained by the writer by irradiating normal male flies and then mating them to females which carried a series of recessive genes along the *X* chromosomes. Any F_1 female which showed one of these recessives must have received from the father either a chromosome in which the normal gene had mutated or a chromosome from which the normal gene at this locus had been deleted (giving "pseudo-dominance"). Subsequently, these aberrant females were tested and individuals carrying deleted chromosomes were analyzed cytologically by a study of the salivary gland chromosomes. For this purpose larvae heterozygous for the deletion were used.

In all of the cases of deletions to be described, an actual absence of a part of the chromosome could be dem-

onstrated but it may be well to mention the genetic criteria used for the separation of deletions. These are recessive lethal effects, pseudo-dominance as explained above, and exaggeration. Mohr[2] has shown that most genes when heterozygous with a deletion (acting in a single dose) show a more extreme (exaggerated) phenotype than when homozygous.

After deletions had been picked up, their genetic limits were tested by matching the deleted chromosome with all available genes in the vicinity of the original locus. All genes showing pseudo-dominance and exaggeration were assumed to be deleted. This test may not always be dependable, however, because, as Mohr has shown, an extreme allelomorph at a given locus (e.g., white) may have the same effect as an actual absence of this locus. It is very important to keep this in mind when making genetic tests, because even though a deletion is demonstrable in the salivary chromosomes it is still possible that an extreme mutation may have occurred just outside the deleted area. The points of breakage of long deletions and translocations were determined by examining hyperploid males and females, and hypoploid females in which the abnormal chromosome, or piece, covered certain recessives. It may be pointed out that as a result of any of these tests we are only able to say that a break lies somewhere in the region between two gene loci. Crossing over tests are of little value in making closer determinations for either translocations or deletions on account of the reduction in crossing over near breakage points.

A number of complex cases have been worked out and have proved to be very valuable but, in general, simple deletions and the simpler types of translocations have been the most useful. Before taking up some of the cytological advantages and difficulties encountered in the use of these, the reader must understand that the relative ease with which we can determine the exact point (or points) at which a chromosome has been broken (or deleted) is due to the fact that in the salivary gland homologous chromosomes undergo somatic synapsis. (In the following work we shall call the cross striations of the chromosomes "bands" or "lines" without prejudice as to their real nature.) For example, in the case of a deletion in the *X* chromosome, the normal *X* will synapse band for band with the abnormal chromosome to each side of the point of the reattachment, causing a buckle in the normal chromosome which corresponds to the lost region, so that we can read right off just what bands are missing (Figure 15*B*). In doing this, however, certain points must be kept in mind. When both breaks of a deletion are within clear areas then the limiting bands are complete and will synapse with ease, so that a mistake as to true homology will not be easily made. However, there are two possible conditions under which one can confuse non-homologous with homologous parts. These are: (a) when one of the breaks has occurred in a clear area and the other within a band, resulting in the formation of a half band, and (b) when each break has occurred within a band, resulting in the formation of a composite band. In these two cases the stretching, compression, and twisting about each other, which is caused by the two chromosomes of different lengths trying to synapse completely, will often cause non-homologous parts to lie side by side and appear to be synapsed. If the above points are kept in mind very accurate determinations of loci are possible by the use of overlapping deletions.

Cytologically there are certain advantages in studying translocations. Since in them no part of the chromosome is lost (at least in non-lethal mutuals), a complete synapsis of all parts is possible. This is a very distinct advantage in making exact determinations, because the possibility of non-homologous parts becoming closely associated is largely eliminated. At

least, this is true when all parts are synapsed to form a cross figure. If in a translocation the break has occurred within a band, the normal band will at times synapse with the half which lies in the left-hand piece, and sometimes with the half which lies in the right-hand piece. Such behavior can then be taken to mean that the break has taken place within the band.

The analysis of one deletion at a particular locus may not place this locus within very narrow limits, but when two slightly overlapping deletions remove the same locus, then a very accurate determination is possible. The same can be said of translocations. If the points of breakage of two translocations practically coincide and genetically a given locus lies to the left of the break in one case and to the right in the other, then the locus is plotted as accurately as we can hope to place it. This implies, of course, that the locus in each case lies very close to the point of breakage. It is on this account that the sort of aberration which has been called "simultaneous breakage and mutation" promises to be of considerable value in mapping chromosomes. The exact rate of occurrence of this type of rearrangement has not been determined, but if the results obtained at the forked locus represent a random sample, then it occurs as frequently as actual deletions. Of a total of nine changes at this locus two proved to be simultaneous translocations and mutations, two true deletions, two mutations accompanied by recessive lethal effects, and three mutations. In the two translocations the forked locus has been shown to be very close to the point of breakage, but in each case to the right of the break. If in one of these the locus had been to the right and in the other to the left of the break then, since the two breaks practically coincide, the locus would have been placed very accurately. It may later be shown that the points of breakage in such cases can be taken as the exact locus of the mutated gene with a fair degree of accuracy and certainty.

Description of Cases and the Limiting of Loci

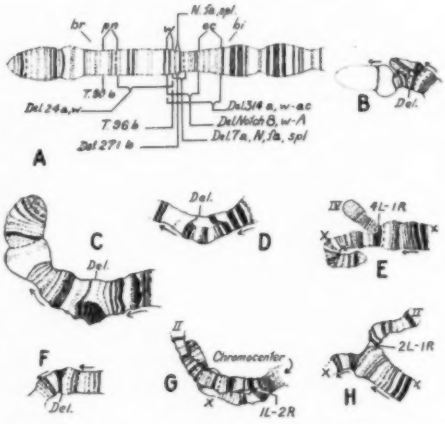
Before taking up each case separately a few points concerning the figures will be mentioned. A camera lucida drawing is given of each case analyzed. The course of the normal chromosome is indicated by arrows, and the points of reattachment in the abnormal elements by lines running up to their margins. If a deletion has occurred this line is labeled "Del." (Figure 15*B*). If a translocation has occurred the chromosome parts involved are given as in Figure 15*E*, for example 4L-1R means that at this point the left piece of the IV chromosome is attached on to the right piece of the *X*. In order that the breaks involved in certain cases may be easily compared they are diagrammatically reproduced upon sections of the complete map (example, Figure 15*A*). On these the points of breakage of translocations are indicated by lines, deleted sections by brackets below the chromosome, and the narrowest limits to which certain loci or groups of loci have been localized are indicated above the chromosome. All these gene localizations are reproduced on the complete morphological map (taken from Painter[7]) shown in Figure 17*J*. This figure also gives all the available data on gene localizations in the *X* chromosome obtained to date, at this laboratory.

The prune locus

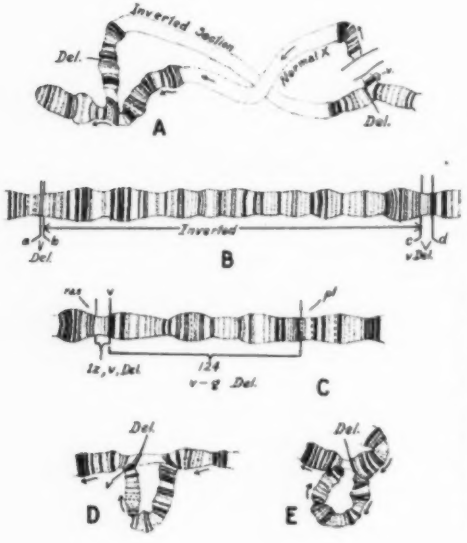
T 1-2, 50b A. This translocation consists of a long deletion in the *X* chromosome with the deleted section inserted into the right arm of the II chromosome. The left break genetically, occurred between broad (*br*) and prune (*pn*), and the right break between rudimentary (*r*) and forked (*f*). Cytologically the left break occurred as is shown diagrammatically in Figure 15*A*. This case will be described in more detail in connection with the forked locus.

SYNAPSIS OF NORMAL AND DELETED CHROMOSOMES

Figure 15



A—This is a section of the *X* chromosome map on which the aberrations illustrated below (*B-H*) are shown diagrammatically. Below the chromosome, translocation breaks are indicated by single lines and the limits of deletions by brackets. Indicated above the chromosome are the narrowest limits to which the genes studied have been localized. *B-H* are camera lucida drawings showing how the various deleted or aberrant chromosomes synapse with a normal *X*. The course of the normal *X* is indicated by arrows. *B* is taken from a female larva heterozygous for deletion 24a. In like manner *C* is taken from Notch 8, *D* from deletion 314a, *E* from T 1-3-4, 96b, and *F* from deletion 7a. *G* and *H* are taken from deletion 271b. The synapsis of the 1L-2R element with the normal II is shown in *G* and in *H* we can see how the 2L-1R element unites with the unbroken *X*.



THE 1z AND THE T 1-2, 124 ABERRATIONS

Figure 16

The aberration known as 1*z*, resulted in the inversion of a part of the *X* chromosome which was accompanied by a deletion at each end of the inverted section. *A* shows the synapsis of a normal with the aberrant *X*. The points at which parts of the chromosome were removed are indicated by *Del*. The inverted section lies between these two labels. *B* is a section of the normal map of the *X* showing diagrammatically just what occurred in the 1*z* aberration. *C* is a section of the normal *X* showing schematically how the vermilion locus is restricted to part of a compound band. In aberration T 1-2, 124 a section of the *X* was deleted and inserted into the second chromosome. *D* shows the synapsis of this aberration with a normal *X*, complete for the left hand side of the break while *E* shows synapsis to the right of the break.

Del. 24a A, genetically removes white but not prune, split (*spl*) or facet (*fa*). Cytologically the deletion (Figure 15*B*) begins three bands to the right of the 50b break and extends through the first two of the five bands which have been termed the "facet" bands by Painter.[4] Figure 15*A* shows diagrammatically just what portion of the *X* was deleted. The evidence from these two cases (50b and 24a) limits the prune locus to the area of the three bands indicated in Figure 15*A*.

The loci of white, white-mottled and echinus

Mohr's Notch 8 genetically removes white (*w*), facet and Abnormal abdomen (*A*), but not prune and echinus (*ec*) (Mohr[2]). The split locus has also been tested for and found to be absent. Cytologically (Figure 15*C*) this deletion removes the right four of the five "facet" bands and a region to the right including two sharply defined dark bands. This is shown diagrammatically in Figure 15*A*. The evidence from this deletion with the foregoing (24a) limits the white locus to the neighborhood of the second of the five facet bands.

Del. 314a A, of Patterson[8], genetically removes white to echinus inclusive, but not prune and bifid (*bi*). Morphologically the left break occurred between the first and second of the facet bands (Figure 15*D*). In this figure the first and second facet bands of the normal chromosome are almost completely fused to form one wide band, and it will be noticed that only the left part of this wide band is present in the abnormal chromosome. Bands 3 and 4 of the facet area are also fused. Such a fusion is often characteristic in this region. The right break occurred just to the left of the first of the three heavily staining bands which have been termed the "three banded area" by Painter. The limits of this deletion compared with those of Notch 8, places echinus within fairly narrow limits (Figure 15*A*). The deleted piece of 314a is inserted in the left arm of the third chromosome and gives a white-mottled effect when present in a female homozygous for white. This places white-mottled within the limits of this deletion.

T 1-3-4, 96b A. This is a complicated translocation in which the *X*, III, and IV chromosomes are involved. Although this case is not yet completely worked out it is known that the break is between white-mottled and facet, that white-mottled and gray are linked with the third chromosome and that most of the IV chromosome is attached to the proximal piece of the *X*. Figure 15*E* shows the 4L-1R element synapsed with the normal *X*. Since only the right three of the facet bands are synapsed the break must have occurred between the second and third facet bands. This is shown diagrammatically in Figure 15*A*. The evidence from this case and the foregoing (314a) places white-mottled on the same band with white, and thus we have independent confirmation as to the locus of white since white-mottled is an allelomorph of this gene.

The loci of Notch, facet and split

Del. 7a A, genetically shows Notch (*N*), and removes facet and split, but not white and echinus. Abnormal abdomen was not tested. Morphologically the right three of the five facet bands are removed (Figure 15*F*). The loci of Notch, facet and split must therefore lie within these three bands as is shown diagrammatically in Figure 15*A*.

Del. 271b A, of Patterson,[8] is a mutual translocation between the *X* and left arm of II with a deletion at the point of breakage in the *X*. It shows Notch, and when crossed to facet and split these two genes are exaggerated. The deletion has not been demonstrated morphologically, but the break and reattachment occurred between the third and fourth facet bands (diagrammatically shown in Figure 15*A*). Figure 15*G* shows the 1L-2R element synapsed with the normal second. Here the left three of the facet bands can be clearly seen to the left of the

point of reattachment. In Figure 15*H*, where the 2L-1R chromosome is shown synapsed with the normal *X* we see the fourth and fifth facet bands synapsed with the normal *X*. A part of the clear area between bands three and four of the facet area must be deleted and it is very possible that some part of one or both of the limiting bands has been lost. The exact limits of such a deletion are extremely difficult to demonstrate. We can only say at most that the loci involved lie within a region including parts of the third and fourth facet bands (Figure 15*A*).

The cut locus

T 1-4, 12A. This is a complicated case found and analyzed genetically by Stone,[10] and cytologically by Painter,[4] The cut (*ct*) locus has been deleted from the *X* and inserted into the left arm of the II chromosome. Genetic tests show that this piece does not include singed (*sn*), ocelliless (*oc*) or carmine (*cm*). The morphological limits of this insertion have been revised as shown in Figure 17*J*.

The vermilion locus

Del. 1*z* A, genetically removes vermilion (*v*), but not raspberry (*ras*) or lozenge (*lz*). When this case was examined cytologically it was found that it involved an inversion with a short deletion at each end of the inverted section. The right break is within a wide heavily staining band labeled *v* in the figures, which has been called the "vermilion" band. In Figure 16*A* three components are visible within this band on the normal chromosome, a heavily staining one in the middle and a lighter one to each side. The right and the middle ones are apparently synapsed, but the left one is clearly missing on the abnormal chromosome. In Figure 16*B* the four breaks are indicated schematically on a section of the map, and using this as a guide the reader can follow the patterns in Figure 16*A*. The regions from *a* to *b* and from *c* to *d* are deleted and the section between *b* and *c* is inverted. This case then shows that vermilion must lie within the deleted area indicated diagrammatically in Figure 16*B*.

T 1-2, 124 A. This case involves a deletion in the *X* chromosome with the deleted section inserted into the right arm of the second chromosome. Genetic tests made by Bedichek (see Patterson et al.[9]) show that vermilion and garnet (*g*) have been deleted, but cut and pleated (*pl*) have not. The fact that the II chromosome carries the normal allelomorphs of vermilion and garnet excludes the possibility of a mutation to vermilion at the left point of breakage. The vermilion locus must therefore be to the right of the left point of breakage of this deletion, shown diagrammatically in Figure 16*C*. In Figure 16*D* we see the left end of the deleted X completely synapsed with the normal up to the point of reattachment, and in Figure 16*E* a complete synapsis of the right end. The point of reattachment in the abnormal chromosome is indicated by "Del." In both figures this line separates a lighter band to the left from a darker one to the right. The lighter band has been interpreted as the left-hand part of the vermilion band. The left break of 124 and the right break of 1z practically coincide, as is shown diagrammatically in Figure 16*C*, and since in 124 the vermilion locus is to the right and in 1z to the left of the break, the vermilion locus probably lies in the left part of the vermilion band. (The word "probably" is used here because it is possible, though not probable, that in Del. 1z a mutation might have occurred near the point of breakage which would be indistinguishable from a deficiency, because vermilion does not display the exaggeration phenomenon).

The forked locus

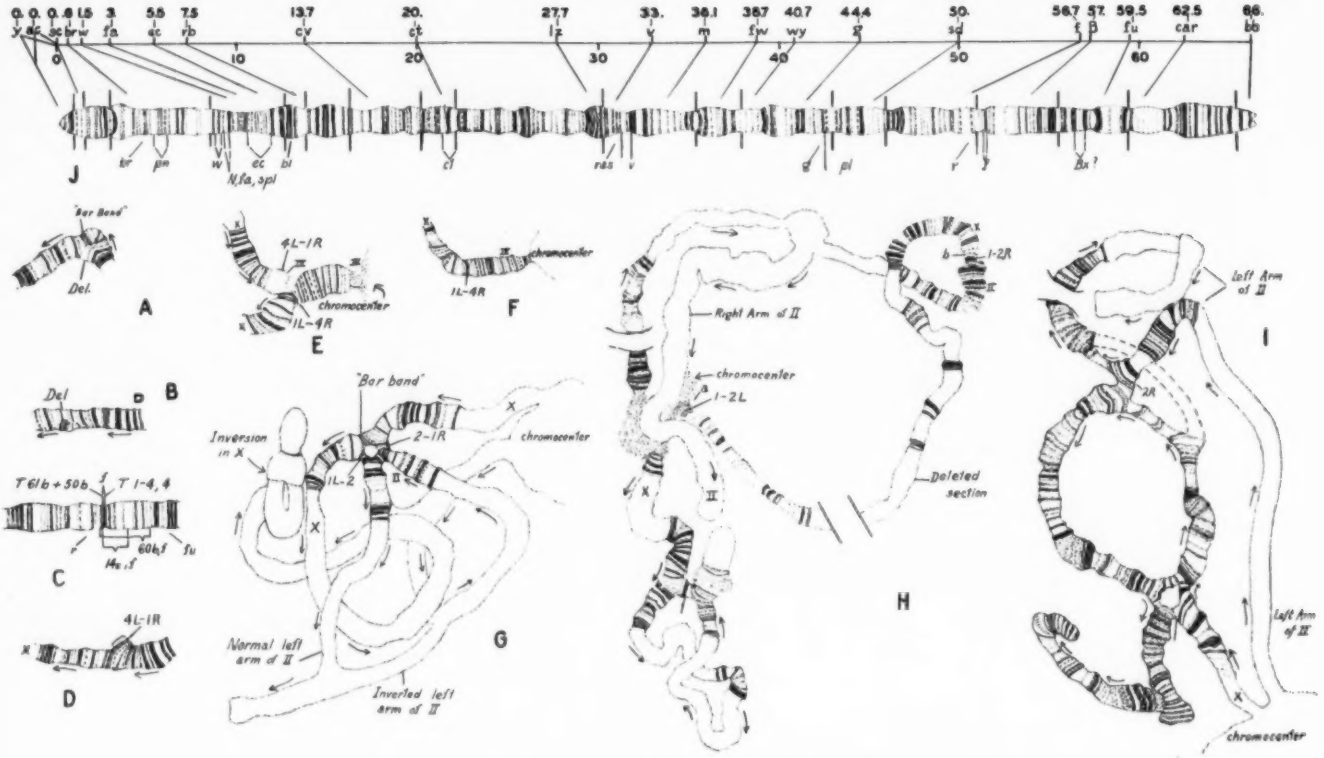
Del. 60b A, and 14z A, both remove forked (*f*), but not rudimentary (*r*) or fused (*fu*). They are both simple deletions which are sufficiently explained by the Figures: 60b in Figure 17*A*, and 14z in Figure 17*B*. Morphologically both remove a heavily staining band near their left limits

which will for convenience be called the "Bar" band provisionally. 60b takes out the first and second bands to the left, and 14z only the first band to the left of the "Bar" band. The limits of these deletions are shown diagrammatically in Figure 17*C*.

T 1-4, 4 A. This translocation was found by Stone and analyzed genetically by him. The *X* is broken between the loci of forked and Bar (*B*), the left end being translocated to the IV chromosome. A preliminary cytological analysis was made by Painter[4] by a study of males. Further study of this case in females has resulted in placing this break within the heavily staining "Bar" band as is indicated schematically in Figure 17*C* Evidence that the break is within this band and not to one or the other side of it is given below.

Figure 17*D* was taken from a female larva hyperploid for the 4L-1R element. The 1R piece is completely synapsed with the two normal *X* chromosomes from the spindle fiber end through the Bar band. The unsynapsed nipple to the left of the Bar band represents the tip of the IV chromosome. In this figure the break seems to have taken place just to the left of the Bar band, but in reality it has occurred within this band as is revealed by a study of Figure 17*E*. This figure (17*E*) shows the 1L-4R chromosome synapsed with the normal *X* and the normal IV chromosome. The tip of the normal IV passes underneath the *X* at the point of reattachment so that it is not visible in the figure. The important point here is that the Bar band of the normal chromosome synapses with what must be a part of the Bar band in the 1L-4R element. Furthermore in nuclei in which the 1L-4R element is not synapsed a dark band is seen at the point of reattachment, which is very obviously not a part of the normal pattern of the fourth (Figure 17*F*). Since at times the normal Bar band synapses with a band to the left of the break and at other times with a band to the right of the break we must conclude that the Bar band has been split by the break. The forked locus therefore lies to the left, and the Bar locus to the right of a point within the Bar band. Since there is only three-tenths of one per cent. crossing over between these two loci, their position must be very close morphologically to the point of separation.

T 1-2 61b, A. This is a mutual exchange with an inverted left arm of the II chromosome. The break is near forked and accompanied by a mutation to forked. That this is a true mutation and not a deficiency is shown first, by the fact that it does not cause forked to be exaggerated when crossed to this gene, as the true deficiencies do at this locus, and second, by its behavior in hyperploid females, which is described below. To determine whether the forked gene is in the left or right piece, hyperploid tests were carried out. These tests are based upon the fact that most forked allelomorphs are hypomorphic according to Muller's[3] classification, that is, their action is toward normal so that a diploid forked female shows a less extreme phenotype than a forked male, and a triple *X* forked female is less forked than the diploid forked female. That this behavior is a function of the gene itself and not of modifying factors in other parts of the *X* has been shown by the following considerations. That the region to the right of forked has no effect is indicated by the fact that yellow, vermilion, forked attached *X* females hyperploid for the right end of translocation 1-4, 4 broken between forked and Bar, are no less forked (only two forked genes present) than the plain yellow, vermilion, forked attached *X* females. The evidence that the region to the left of forked has no effect comes from 61b itself. Hyperploid females containing two forked chromosomes plus the left-hand piece of this translocation are just as forked (only two forked genes present) as diploid forked females. That the forked gene lies in the right piece in 61b is



DELETIONS AND TRANSLOCATIONS OF THE *X* CHROMOSOME

Figure 17

A shows deletion 60b synapsed with a normal element; and *B* deletion 14z. In *C* we have a section of the normal *X* showing diagrammatically the breaks near the forked locus. *D*, *E*, and *F* are drawings of the 1-4, 4 translocation, for explanation see text. *G* shows the aberration known as T 1-2, 61b partly synapsed with a normal *X* and second chromosome, which is explained in the body of this paper. *H* and *I* are complex aberrations known as T 1-2, 50b and T 1-2, 106b. *J*, which is taken from Painter, is a map of the *X* chromosome showing the position or morphological limits of all gene loci which have been placed to date. Single lines on each side of the *X* show approximately where a translocation has broken this element, and lines from the crossover map above the figure of the *X* indicate the limiting gene loci. Below the *X* are brackets or lines showing the position of the genes discussed in the present study.

shown by the fact that hyperploid females containing two forked chromosomes plus this piece are less forked than the diploid forked females. This means that the hyperploids contain three forked genes.

That the break is very near the forked locus is shown by the fact that it occurred within the region included in the short forked deletion 14z (Figure 17*C*). Figure 17*G* shows the normal *X* chromosome practically completely synapsed with the 1L-2, and the 2-1R chromosomes. Here we see the proximal region of the *X* synapsed from the spindle fiber end up to and including the heavily staining Bar band. Just distal to the Bar band of the normal *X* are two lighter staining bands (almost completely fused in Figure 17*G*). The most distal of these is clearly synapsed, but the proximal one which for convenience in description will be called the "forked" band, appears to be only partly synapsed. The unsynapsed proximal portion has been interpreted to be homologous with the fine band which is seen just distal to the Bar band in the 2-1R chromosome. A more complete synapsis than is shown in this figure has never been seen and it would probably be useless to continue to search for better synapsis on account of the complexity of the case. According to the above interpretation the break occurred within the band which has been called the "forked" band, and the forked locus lies to the right of this break as is shown diagrammatically in Figure 17*C*.

T 1-2, 50b A, consists of a deleted *X* chromosome with the deleted section inserted into the right arm of the second. The left break is between broad and prune, and has already been described (Figure 15*A*). The right break is just to the left of forked and is accompanied by a mutation to forked. That this is a true mutation and not a deficiency, and that the forked gene lies to the right of this break was demonstrated by tests similar to those carried out with 61b. The complete configuration of this abnormality, partly synapsed with the normal chromosomes, is shown in Figure 17*H*. In the lower left-hand corner the deleted *X* is shown synapsed with the normal *X*. The right end of the deleted section, which is entirely unsynapsed, apparently arises from the chromocenter at *a* and continues to the upper right-hand corner of the figure where the left end of this section attaches on to the proximal end of the right arm of the second, which soon synapses with the normal second. Beginning at the spindle fiber end of the *X* we find the proximal portion synapsed almost to the heavily staining Bar band. In other preparations good synapsis of this band has been seen. In the deleted *X* there is a fine lightly staining band just distal to the Bar band, which has been interpreted as the proximal portion of the forked band. There are three reasons for this interpretation. First, no such lightly staining band has ever been found associated with the Bar band even when this region is stretched. Second, it is lighter and finer than the normal forked band. Third, it cannot be a part of the most distal band of the deleted section indicated at *b* in the upper right corner of the figure, because a clear space exists between this last band and the pattern of the II chromosome. It should be added that near the attachment of this arm of the normal II chromosome to the chromocenter no areas as clear as this are ever seen. Therefore the left break must have taken place within this clear area of the normal chromosome as indicated diagrammatically in Figure 15*A*. At the other end (proximal end) of the deleted section which arises from the chromocenter, a pair of bands is seen which has been interpreted as homologous to the pair just distal to the Bar band. The most proximal of these is the "forked" band which is not quite complete if the interpretation given is correct. The evidence gathered from these three cases, translocations 1-4 4, 61b and 50b, places the forked locus between a point within the "forked" band and a point within

mes from the crossover map above the figure of the X chromosome and showing genes discussed in the present study.

the "Bar" band as indicated diagrammatically in Figure 17*C*.

T 1-2, 106b, A. This is a complicated case in which a long deletion has occurred in the *X* chromosome and the deleted section has been inserted into the left arm of the second. In Figure 17*I*, we see the deleted *X* chromosome completely synapsed. The circle in the center of the figure represents the deleted portion almost completely synapsed with the normal *X*. Beginning at the chromocenter the left arm of the second is synapsed up to about the middle of this arm. Here the deleted section of the *X* attaches on to the 2R piece, and as we follow the deleted section around the loop we come first to the point where the loop was closed when the deletion was formed, and then to the point where this loop should attach on to the distal half of the left arm of the second. This connection has been reconstructed with dash lines for the sake of completeness. This case is a very good demonstration of the manner of occurrence of long deletions. The deleted loop would of course have been lost if it had not been inserted into the second. Short deletions might occur in the same manner. It will be noticed that the parts of this insertion are not in normal sequence. This figure also illustrates how an insertion may occur such as that in 50b, where all parts of the whole deleted-inserted section are apparently in normal sequence. For example if the translocation of 106b had occurred very close to the point of breakage and reattachment of the deleted loop of the *X*, the sequence would still be abnormal but one of the sections would be too small to be recognized. The result would be an insertion with all of the inserted portion apparently in normal sequence.

This stock was originally picked up as a Beadex (*Bx*) mutation. When the salivary gland analysis revealed a break and reattachment near the expected neighborhood of the Beadex locus, it was assumed that this was another case of breakage accompanied by mutation, such as those at the forked locus, and the Beadex locus was tentatively placed in the region of this break (Figure 17*J*).

Discussion

Among the many problems which the use of salivary glands have allowed us to attack none is more important than the exact localization of gene loci along the chromosomes. Since this problem will be one of the foremost in the field of cyto-genetics until most of the genes have been accurately located in *Drosophila melanogaster*, it is pertinent to discuss the relative merits of the translocation and deletion methods.

Translocations occur frequently and are easily detected, but the disadvantage with these is the difficulty of determining exactly, genetically, the point of breakage. Unless hyperploid flies will live, and the experience of this laboratory is that autosomal hyperploids usually do not survive, then laborious crossover counts must be made and unusually large numbers are required. In addition there is some evidence that the breaks tend to occur in definite regions, at least in 2-4 and 3-4 translocations, as if there was a rather definite orientation of the elements in the sperm head at the time of irradiation, so that many breaks may be bunched within narrow morphological limits (see Patterson et al.[9] and Painter[5,6] for examples). These factors make translocations a less desirable method than the use of deletions, but when the former are available and have been analyzed genetically, they offer a quick method for determining the morphological limits within which a given gene must lie.

Deletions, like translocations, occur frequently as a result of irradiation and they offer a more direct method of locating gene loci. They are easily picked up, can be tested genetically very readily, and with the proper genetic set-up limited regions of a chromosome can be investigated. There are, however, certain pitfalls to be

avoided when deletions are studied, i.e., possible confusion concerning homology when one or both breaks fall within bands and the possible occurrence of an extreme mutation (i.e. "amorph" by Muller's[3] terminology) having the same phenotypic effect as a true deletion of this region near the points of breakage. Both of these sources of error have been fully discussed in the body of this paper.

This brings us to the discussion of a type of abnormality which has been found to be very useful and which seems to occur quite frequently, namely, simultaneous mutation and chromosome breakage. The usefulness of this type hinges upon the fact that in the cases analyzed up to the present, the break occurred very near the locus of the mutation, and that therefore breaks near a given locus can be picked up by the same direct method used to isolate deletions and at the same time that deletions are being isolated.

We come now to the question of where the genes are placed. Do they lie within the bands or are they distributed along the matrix irrespective of these chromatic differentiations? This question has not been definitely answered, but the evidence to date is in favor of the genes lying within bands in so far as the maximum limits of each localization include at least part of a band, and up to the present no gene has been limited to within a relatively clear area. It must be pointed out, however, that in each case the inclusion of at least part of a clear area is possible, either to each side of a band or within the chromosome if these "bands" are in the nature of rings rather than disks. Even in the case of vermilion which has been limited to part of a band, this is true, since the wide vermilion band is often seen to be made up of component bands with small clear areas between. If in time many loci are definitely limited to bands and none to clear areas then we may assume with some degree of safety that the chromatic bands represent the gene bearing material.

We have called the chromatic cross striations of the salivary gland chromosomes "bands," realizing from the beginning that they are composite structures, that the wider bands are often seen to be aggregates of several smaller bands, that the finer bands often show a particulate structure similar to a string of beads running around the chromosome, and that these particles are often fused to form a solid band. These finer details of structure are best seen in lightly stained preparations and since it was necessary in the present study to stain deeply in order to bring out faint lines, most of the figures do not show the particulate nature of the bands. It has been felt that the first step in the localization of the gene was the accurate placing of the loci with relation to the visible structures. In his recent paper in this JOURNAL Painter[7] reviewed the various ideas which have been expressed about the nature of these "bands."

The possibility that all lethals are due to small deletions has been suggested and there can be no doubt that many of the abnormalities that have been classed as lethals are in reality short deletions which remove no known loci. Up to the present we have not been able to distinguish between a lethal caused by a small deletion and one caused by a point mutation. The salivary glands of a number of lethal stocks have been examined in which no deletion could be demonstrated. This of course does not exclude the possibility of an undetectable one being present. Dominant Notch stocks have been examined in which no absence could be demonstrated. Here we are confronted with the problem of distinguishing between an actual absence and a possible dominant point mutation, accompanied by a recessive lethal effect, which has the same effect as an actual absence. So far all demonstrable deletions have recessive lethal effects. Therefore, as far as the evidence goes, a lethal may still be either a point mu-

tation or a deletion (visible or invisible).

It has long been pointed out that a large number of translocations are accompanied by recessive lethals. (For a discussion of simultaneous effects resulting from irradiation see Muller.[3]) Just how many of these lethals are due to actual losses of chromatin at the point of breakage, has not been determined. In the one case of translocation accompanied by a forked mutation and a recessive lethal (50b) no deletion was demonstrable. In one case (271b) a deletion probably exists because this stock has a dominant Notch and a recessive lethal effect, and genetic tests show that facet and split are deleted (show pseudo-dominance and exaggeration when heterozygous with the abnormal chromosome).

Since the preparation of this article the work of Bridges on the detailed normal morphology of salivary chromosomes has appeared (*Journal of Heredity*, Vol. 26, 60-64). For the reader's convenience the following readings are given (according to Bridges' system) by which the reader may place the limitations for genes determined in the present paper upon the map prepared by Bridges:

prune	2D6 - 2F2	inclusive
white	3C2	
facet, split, Notch	3C3 - 3C6	inclusive
echinus	3E2 - 3E4	"
cut	7A3 - 7B4	"
vermilion	10A1	"
forked	15E1 - 15F1	"
Beadex	17C1 - 17D1	"

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